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CALAMOPHYTON BICEPHALUM, A NEW SPECIES FROM THE MIDDLE DEVONIAN OF BELGIUM

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ABSTRACT

This paper describes five specimens of *Calamophyton* found in the Middle Devonian of Belgium. Well preserved specimens have revealed the fact that both sterile and fertile appendages branch to form three-dimensional structures which are more complex than was formerly known for the genus. A new species, *Calamophyton bicephalum*, is established in which the sporangiophores bore twelve pendulous sporangia when all developed. SUZANNE LECLERCQ, Université de Liège, Laboratoire de Paléontologie Végétale, 7, Place du Vingt-Août, Liège, Belgium; HENRY N. ANDREWS, JR., Henry Shaw School of Botany, Washington University, St. Louis 30, Missouri.

INTRODUCTION

The fossil plant material on which the present study is based was collected by S. Leclercq in 1949 and 1952 from a Middle Devonian horizon in eastern Belgium. The Middle Devonian in Belgium is divided into the Couvinian and the overlying Givetian and our specimens come from the lower part of the latter.

The fossiliferous horizon is well exposed in one of two quarries (the north one) known locally as the "Carrières Brandt". They are situated on the upper part of the western slope of a hill lying 400 meters south of the junction of the rivers "La Gileppe" and "La Vesdre" at the small village of Goé which is in turn located about 30 kilometers east of Liège and 20 kilometers from Germany. The plant-bearing horizon is a lens-shaped deposit of numerous greenish and grey-blue shale layers 0.1 to 1.1 meters thick which are interbedded with arkose strata. It has been shown that the Middle Devonian in this region is a littoral formation deposited in shallow marine conditions (Aderca, 1932, p. 14; Liegeois, 1956, p. 98).

The fossil remains are abundantly distributed through the shales but the quality of preservation varies with the different layers. In most of them large specimens are encountered while in some the material is more fragmentary. The plants are found for the most part as well preserved compressions and occasionally as petrifications in which the plant tissues are impregnated with iron hydroxide.

The "Goé flora" is a large one and includes many specimens referable to the Protoarticulatae. Some of them are large, splendid specimens representing the

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typical habit of *Calamophyton*; others are more fragmentary and it is problematical as to whether they should be referred to this genus or to *Hyenia*. It is, moreover, very possible that some will prove to lie outside the limits of both genera.

As is often the case in paleobotany our knowledge of these presumed early articulates has accumulated as the result of the work of several investigators and the quality of preservation and relative fragmentary state of the plants dealt with has varied greatly. Due chiefly to faulty preservation previous interpretations are not entirely correct and it seems fair to assert that, in general, the plants are not as well known as some of the published accounts would lead one to believe.

The present investigation was initiated in part from the discovery of the elaborate organization of the sporangiophore of the Upper Devonian sphenopsid cone *Eviostachya boegi* Stockmans which was described in detail by Leclercq in 1957. The unexpected complexity of the sporangiophore "head" of this plant and the availability of well preserved specimens of the Middle Devonian Proto-articulates suggested the desirability of reinvestigating the latter.

Our study is based on several *Calamophyton* specimens which display the typical habit of that plant and the preservation is such that we have had an opportunity to contribute somewhat to a better understanding of the morphology of the leaves and spore-bearing appendages. The latter have proven to be much more complex than was supposed and we have been able to add appreciably to our knowledge of the branching pattern of the leaves. It is thus necessary to review the previous studies, at least briefly, particularly with reference to the presumed differences between *Calamophyton* and *Hyenia*.

PREVIOUS STUDIES

The genus *Calamophyton* was established in 1926 by Kräusel and Weyland with *C. primaevum* as the type species. It is reconstructed as a plant with an upright main stem which branches initially in a more or less digitate fashion; the primary branches, although predominantly monopodial, may also give rise to nearly equal dichotomies (see their plate 15, fig. 2). The leaves are once or twice forked and apparently less filiform than those of *Hyenia*. In view of our own description that follows it is perhaps significant to emphasize this difference as noted by Kräusel and Weyland (cf. their text figs. 26 of *Calamophyton* and 16a, 16b of *Hyenia*). Somewhat stouter, unforked sterile appendages were borne on the "main stem" and on the basal part of the primary branches. The fertile shoots are similar to those of *Hyenia* but each arm of the bifurcated sporangiophore usually bears but one sporangium (cf. their text fig. 27 of *Calamophyton* and text fig. 22 of *Hyenia*). Additional specimens were described by the same authors in their 1929 contribution.

In 1932 Aderca described and figured a fine sterile specimen of *Calamophyton primaevum* which was obtained at the same outcrop from which the new material described herewith was obtained. This specimen will be referred to again but it may be pointed out that it was erroneously determined as *Hyenia elegans* (see

Aderca's pl. 2, fig. 4), although the mistake was corrected by Kräusel (1932, p. 277). In 1940 Leclercq reported *C. primaevum*, as well as a new species, *C. renieri*, from the Middle Devonian of Belgium. She noted (see pp. 18, 33, 35) that most of the leaves in both species were more frequently divided and more filiform than those described for the above mentioned German specimens (cf. Leclercq, 1940, text fig. 9 with Kräusel and Weyland's figures).

The differences between the foliage of *Calamophyton primaevum* and *Hyenia elegans* as indicated by Kräusel and Weyland in the text figures cited above is quite striking; those of *Calamophyton* show a leaf that is narrow, almost wedge-shaped with a notched tip and it is this figure that has been used in textbooks (see, for example, Hirmer, 1927, fig. 400, 401; Arnold, 1947, fig. 55; Walton, 1953, fig. 38; Smith, 1955, p. 241; Magdefrau, 1956, fig. 61). Actually, Kräusel and Weyland's restoration does not bear out this exaggerated difference and in their description the leaves of *Calamophyton* are described as "schmallineal, ein- bis mehrfach gegabelt" (1926, p. 141). Unfortunately their specimens are no longer available for comparison but we shall present additional evidence which suggests that it is very doubtful whether the two genera can be distinguished on the basis of their leaves when only fragmentary specimens are available.

The fertile appendages (sporangiophores) of the two genera were described by Kräusel and Weyland as being very similar. In the case of *Hyenia* each branch of the sporangiophore is said to bear two or three sporangia while only one is found in the corresponding position in *Calamophyton* (cf. their text fig. 22 for *Hyenia* and text fig. 27 for *Calamophyton*). In her 1940 study of certain Belgian protoarticates Leclercq noted that in *Calamophyton* each branch of the sporangiophore usually bore two sporangia; in the *Hyenia* specimens that she then had available the sporangiophores were noted to have several slender, bifurcating distal appendages. This suggested a greater complexity than was reported for the German fossils and is interesting in the light of our present observations which have been made on specimens of vastly better preservation.

As to the general habit of the plants in the two genera, although Kräusel and Weyland's original restoration of *Hyenia* (1926, pl. 16) shows a plant rather similar to that of *Calamophyton*, it was later recognized that the leafy and fertile shoots of *Hyenia* were borne on a relatively massive rhizome (Kräusel and Weyland, 1932, fig. 3). Studies that confirm this type of habit have been made on *Hyenia* specimens from Norway (Höeg, 1945) and Belgium (Leclercq, 1940) and these authors have both supplied restorations that indicate a conspicuous rhizome with slender upright shoots which are usually unbranched.

In summary it may be said, in the light of our present knowledge, that it is very doubtful whether the upright shoots of *Hyenia* can be differentiated from the distal parts of *Calamophyton* and only the general habit of the two remains as a distinguishing character that may be used with assurance. There is thus some question as to whether the two should be generically separated. It may also be noted that the anatomy of the two is not sufficiently well known to shed much light on the problem.

MATERIALS ON WHICH THE PRESENT STUDY IS BASED; STUDY TECHNIQUE

It is evident from the above summary that much remains to be learned about these fossil plants and it is particularly necessary that we have better preserved specimens in order to eliminate the doubt that exists concerning the morphology and taxonomy of these presumed early members of the articulate group. Our investigations have not solved all the problems but we have been able to make the following contributions which add to an understanding of the morphology of *Calamophyton*:

1. The sterile appendages (leaves) dichotomize two to four times and it is doubtful whether they can, with certainty, be distinguished from those of *Hyenia*.
2. The sterile appendages are three-dimensional in their branching pattern.
3. The fertile appendages are much more complex than previous accounts indicate.
4. Both fertile and sterile appendages may be borne on the same branch; there is, however, a marked tendency for the fertile appendages to be aggregated together into an apparently specialized branch system, but not into a clearly defined "cone".

The specimens that have been studied and the names assigned to them are as follows:

Calamophyton bicephalum Leclercq and Andrews, sp. nov.: Nos. 5011/609, 5012/337, 5009/588, 5007/346. In all cases the first of each dual number is the permanent one assigned to the fossil and the second is the number originally given in the field).

Calamophyton primaevum Kräusel and Weyland: No. 5006, previously described by Aderca, 1932, pl. 11, fig. 4.

Since the technique that is employed in the investigation of these fossils, although very simple, is perhaps not widely known, a brief description seems appropriate. The plants are preserved as compressions and both fertile and sterile appendages were three dimensional in their branching patterns. Since they also possessed some rigidity a single appendage may extend through several millimeters of sediment, thus it is not possible to apply a transfer technique and remove the entire specimen. What is revealed when the rock is first split gives at best a partial picture of an appendage as we shall point out in some detail in the descriptions. It is thus necessary to follow, through both part and counterpart, a selected appendage in order to determine its three-dimensional form. In the case of the fertile appendages, due to their small size and complex branching pattern, it often becomes necessary to excavate the matrix in terms of fragments only a few microns in diameter. Mechanical vibratory devices are much too coarse for such a delicate degagement and it is accomplished with steel needles and a small, light weight hammer. The size of the needles and the shape of the point will depend on the nature and delicacy of the operation. Invaluable information may thus be obtained with careful, painstaking work and the only costly element involved is the worker's time.

GROSS MORPHOLOGY OF THE BRANCH SYSTEM

Reference will be made first to figure 1 (No. 5012/337) which is the largest

and most complete specimen insofar as the branch system as a whole is concerned. This consists of a major axis two cm. in diameter which divides repeatedly; since it is shown natural size in the figure it does not seem necessary to cite measurements for the various branch orders. It should be noted that the ultimate basal part of the plant is not preserved nor has this been identified in any other specimens. We shall, however, as a matter of convenience in description, refer to this basal part of the specimen as the *main stem*, and the first division members as the *primary branches*.

Although the initial branching of the main stem in a more or less digitate fashion seems to be highly characteristic of *Calamophyton* there is some variation in the organization of this cluster of primary branches. In figure 1 the main stem divides to form two unequal branches and the latter continue to dichotomize more or less equally throughout the length of the specimen. In the specimen shown at the upper left of figure 7 the main stem produces, almost simultaneously, seven primary branches of nearly equal diameter; the main stem of the specimen in the lower right of this figure starts with an equal dichotomy and the primary branches quickly divide again. In figure 14 the main stem produces three primary branches, although it might be interpreted as an initial unequal dichotomy in which the larger branch to the right dichotomizes again about two mm. above the initial division. The rather broad diagonal white band running through the upper part of the main stem represents a slight fault in the rock.

It is important to note that the main stem in fig. 1, and to a lesser degree the basal portion of the primary branches, shows the transverse bands which have been cited as a characteristic feature of *Calamophyton*. Several of these striations are preservation artifacts although some suggest an internal structure possibly comparable with the higher articulates; they are not evident in the upper branches of the specimen. Less clearly defined bands are present in the larger specimen (upper left) of fig. 7; we have not observed the transverse bands in the other specimens at our disposal. It also seems significant that in the basal part of this specimen (fig. 1) the striations are not correlated with any regularity in the distribution of the sterile appendages; thus if it is assumed that the transverse striations indicate nodes the leaves are scattered irregularly through the internodal region. Therefore we do not feel that there is sufficient evidence to regard this character as distinctive of *Calamophyton* and there is not adequate reason for comparing them precisely with the characteristic nodal structure of articulates such as the calamites and *Equisetum*.

THE STERILE APPENDAGES (LEAVES)

A. ON THE MAIN STEM

The sterile appendages or leaves on the main stem are somewhat more robust than those borne higher up on the plant. Some appear as simple unforked structures, others are branched while some represent only the basal portions of branched leaves. The best preserved examples were found on specimens Nos. 5012/337 (fig. 1) and No. 5011/609 (part and counterpart, figs. 20 and 21). Some leaves of

No. 5012/337 are reproduced at a magnification of $\times 5$ on plate 1; they represent the appendages shown in fig. 1 at points *a* (fig. 2), *b* (fig. 3), *c* (fig. 4) and *d* (fig. 5). It will be noted that the most profusely branched leaf reached four orders of divisions and was found higher up on the stem than the other examples cited.

One leaf was found on the main stem of the right hand specimen shown in figure 7 (point *a*) which contained a clearly defined vascular strand which could be followed almost to the tip. This leaf is shown enlarged in fig. 11 and a portion of the vascular strand is shown in fig. 10; the tracheids are apparently of the annular type.

In specimen No. 5011/609 (fig. 20) the leaves display a tendency toward a whorled arrangement but it seems significant to note that the transverse bands, previously considered as characteristic of *Calamophyton*, are not evident here and, as we have noted above, the transverse bands in the stem in fig. 1 are not correlated with any regular arrangement of the leaves.

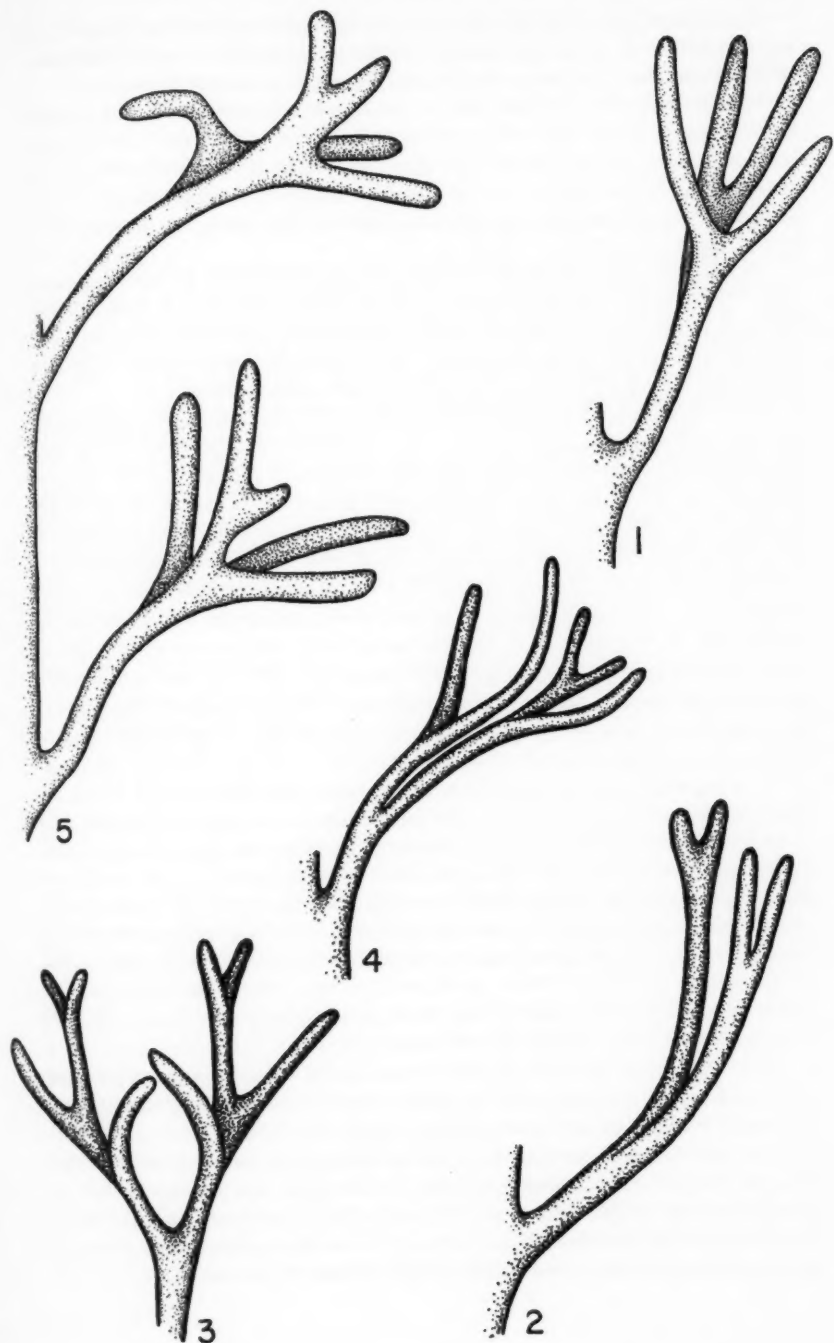
B. ON THE BRANCH SYSTEM ABOVE THE MAIN STEM

It is important to note that, prior to degagement, specimens give a misleading picture of the leaves since only about half of the appendage is exposed by the initial split of the rock specimen; this has been noted for other Devonian fossils in previous studies by Leclercq (1940, 1957). Consequently a considerable number of leaves were degaged or excavated with a small hammer and fine steel needles. Leaves were selected for detailed study that appeared to be well preserved and that were clearly identifiable on both part and counterpart. The leaf was degaged away, starting at the distal end, and followed toward the point of attachment to the stem until a branch was encountered. When this was done to both part and counterpart no question remained as to whether the entire leaf had been revealed. This resulted in the partial destruction of some leaves but the results obtained fully justified the procedure.

In several instances we were fortunate in obtaining the desired information without destruction of the leaf. Figure 8 shows a leaf from specimen No. 5009/588 (fig. 7, *b*) which appeared initially with the Y-shaped terminal portion (*a*) attached at point *b*. Due to a fortunate cleavage of the rock it was possible to remove this terminal portion intact and a comparable branch *c* was revealed directly underneath. The chip was glued in position as shown in the photo, thus preserving the entire leaf. In summary then, we are dealing with a leaf that forked at point *b* to form two equal branches (*a* and *c*) and the latter in turn dichotomize at right angles to the first dichotomy. A restoration of the leaf is shown in text fig. 1. Several other fortunate excavations of this sort revealed the same three-dimensional branching pattern without destruction of the leaf.

Several other examples, also taken from specimen No. 5009/588, will be mentioned to record variations in the gross morphology of these leaves:

Text figs. 1-5. 1. Restoration of leaf shown in fig. 8. 2. Restoration of leaf shown in fig. 7 at *c*. 3. Restoration of upper leaf in fig. 13. 4. Restoration of leaf shown in fig. 12. 5. Restoration of leaves from specimen No. 5006 shown in figs. 15, 16.



Text figure 2 shows another leaf from the right hand specimen in figure 7 (e); this is similar to the preceding example but the initial dichotomy takes place closer to the proximal end and the secondary forking results in shorter branches.

Figure 12 shows a leaf attached at point *c* in figure 7. This was revealed initially, partly in side view and partly in surface view, and no further excavation was conducted. The leaf divides first at *a*, and then both branches divide at right angles to the first division at *b*. At the upper of the *b* divisions one of the two secondary branches was lost but this is indicated in the restoration drawing given in text fig. 4.

The upper portion of figure 13 shows another leaf from the same specimen (fig. 7, *d*). In this case the entire leaf was exposed initially and it is included to illustrate an example in which four orders of branching are evident; it is shown in text fig. 3 as an aid in interpretation. This represents the maximum degree of branching that we have observed in the leaves of *Calamophyton*.

Other leaves with four orders of branching have been carefully uncovered on the part and counterpart of specimen No. 5009/588 (figs. 9, 19). When well preserved they appear similar to the one shown in fig. 13 and text fig. 3. Another example (fig. 5) of one with four orders of branching is shown in the fertile specimen No. 5012/337 at point *d*. It is important to note that the leaves inserted in a similar position on a sterile branch system were small and wedge-shaped.

Many other examples could be cited but they would only duplicate the results obtained from those cited above. The ones chosen reveal the typical branching pattern and the variations that are encountered with reference to the number of orders of branching. There are numerous examples of the type shown in figure 8 and occasional variants from this pattern reveal a lack of forking of the secondary branches but the examples shown in figures 9, 12, 13 and 19 with three or four orders of branching seem to be most typical.

It is pertinent next to summarize the evidence that indicates the leaves are three-dimensional structures. In most cases it could be observed that the first dichotomy resulted in two branches that were directly superimposed; this is well shown in figure 8 where branch *a* was directly above branch *c*. In the second division, however, the resultant two segments lie apparently in the same bedding plane. In most cases where two or more orders of branching were present we are virtually certain that the orientation of successive branchings was at right angles, except possibly the fourth order. Additional evidence comes from examples such as the one in figure 12 (text fig. 4) in which irregular fracturing of the rock revealed a leaf initially in side and surface view.

There is next the question of the cross-sectional shape of these appendages; they are shown in the restorations as having been terete and we feel that there is substantial evidence to indicate that this was the case.

First, the leaves must have had considerable rigidity to have retained their three-dimensional form during fossilization. As many degagements reveal, one primary segment pushed down into the accumulating sediments so that the leaf as a whole was not flattened into one plane. It seems most unlikely that this would have been possible if the leaves had been thin, laminate structures.

Second, in well preserved specimens the thickness of the carbonaceous film is somewhat greater than might be expected if the leaves were laminate.

Third, for whatever correlation purposes it may be worth, it may be noted that several early land plants that are known in the petrified state (*Rhynia*, *Horneophyton*, at least some *Coenopterids*) possessed a shoot system in which the ultimate branches are terete.

THE FERTILE APPENDAGES (SPORANGIOPHORES)

The quality of preservation of the fertile appendages varies considerably and this is due in part to their relative state of maturity at the time of fossilization. Our most significant evidence has come from specimen No. 5011/609 in which the preservation is excellent and the sporangiophores retain most or all of their sporangia. In contrast to this, specimen No. 5012/337 seems to be one in which dehiscence took place some time prior to fossilization; most of the sporangia are shriveled, fragmentary or missing.

Our basic description will, therefore, deal with a well preserved and apparently complete appendage from No. 5011/609. This is supplemented with a description of a second appendage of this specimen as well as several from No. 5012/337, partly to illustrate minor variations in the morphology of the fertile appendage and differences that result from the preservation of specimens at different states of maturity.

SPECIMEN NO. 5011/609

The fertile branch system as a whole is shown natural size in figure 21, the general morphology of the specimen being essentially the same as that found in the specimens shown in figs. 1, 7 and 14. It consists of an upright main axis of about 7 mm. in diameter which, at the top, divides into three primary branches which are of about the same size. One of the branches is dichotomized. The ultimate basal and terminal portions of the specimen are not preserved.

Below the point of division the main axis bears sterile, rigid appendages. These represent for the most part only the basal portion of the whole appendage; some are more complete and display a part of the more distal, divided portion. These organs are similar to the "basal leaves" found on the main axis of specimen No. 5012/337 (fig. 1).

The primary branches of the specimen are fertile throughout the portion that is preserved (fig. 29). They bear many whorls of sporangiophores only, there being no associated bracts. It has not been possible to determine the number of sporangiophores in a whorl; there are at least three and possibly as many as six. It was also difficult to decide whether, in successive whorls, the appendages were superimposed or alternate, though it is more probable that they were superimposed.

It is important to note that here, as in the case of the sterile appendages, the initial exposure of the specimen gives a misleading picture of the general morphology of the sporangiophore. The latter is a three-dimensional structure and half or more of it may be covered by the rock matrix. In order to be sure of

arriving at a correct understanding of the sporangiophore many of them were carefully uncovered under a binocular microscope using needles and a light weight hammer as described above.

Successive stages in the degagement of a selected sporangiophore are illustrated in figures 23 to 27. Figure 22 represents the counterpart (specimen No. 5011/609B) of the initial stage shown in fig. 23. As an introduction to the detailed description it may assist the reader to note briefly the over-all branch pattern: the fertile appendage divides into two segments or "heads" (referred to as upper and lower), each of which bore three short side stalks and each of these in turn terminates in a pair of sporangia; the distal tip of each of the two segments is usually bifurcated but not always so. Thus the sporangiophore as a whole, composed of two similar heads, supports twelve sporangia if all develop.

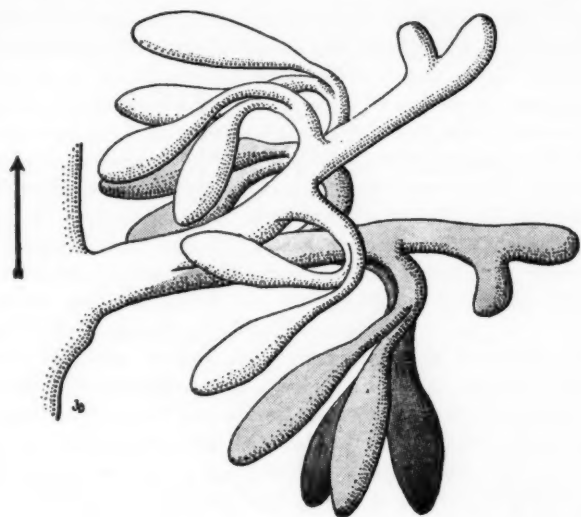
In figures 22 and 23 the upper segment (I) is shown from its base up to the ultimate preserved tip. This segment supports two side stalks, A and B, which are attached on either side at slightly different levels; two sporangia are borne on each stalk (fig. 23 and text fig. 6). Figure 24 reveals the third stalk, C, of the upper segment and one of its sporangia is visible; the second one is still overlain by stalk B although its distal part appears beside the two sporangia of the B stalk. Text figure 6 shows this upper segment or head with the three bifurcated stalks and their six sporangia in the position in which they were preserved.

In figure 24 a portion of the lower segment or head may be seen behind the upper one. Figure 25 shows the lower segment (II) in connection with segment I as well as the three stalks A, B, and C, which are borne by it (segment II); this is also shown in text figure 7. Stalk A has two sporangia in connection; stalk B appears with one sporangium attached and the second lies under segment I; stalk C is just coming into view at this level. In figures 25, 26 and 27 the second sporangium of stalk B has been revealed by removing parts of segment I. Stalk C, which was recurved under segment II, has been uncovered by destroying parts of the latter; it is now clearly revealed and has one sporangium suspended in an anatropous position on each of its two divisions or pedicels. Text figure 7 shows this lower segment (II) with its three bifurcated stalks and their six sporangia.

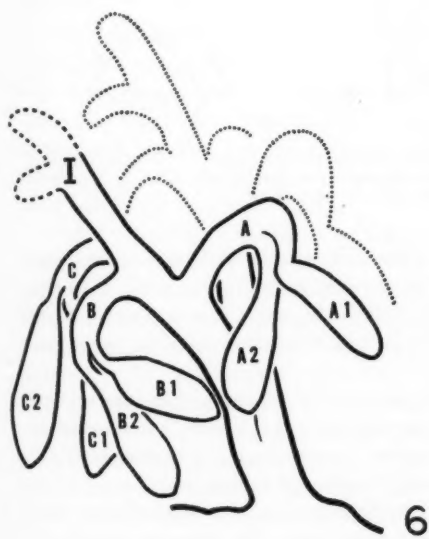
Text figures 6 and 7 when superimposed show the entangled stalks and sporangia of the entire sporangiophore as it was embedded in the sediment; text figure 8 is a reconstruction of the sporangiophore as we believe it appeared before fossilization and in natural position.

Thus, in summary, the sporangiophore was a small, adaxially inclined appendage attached to the branch axis. At a point about one third of the way from its proximal end the sporangiophore branched into an upper and lower segment. Each segment was erect and rigid and supported three short side stalks fixed at two different levels; the first stalk was given off at a different level than the two others which appear generally to be given off simultaneously. Each of the three stalks is slightly bifurcated at its tip with a sporangium attached to each bifurcation. Usually the distal, rigid portion of each segment of the sporangiophore terminates in an irregular dichotomy.

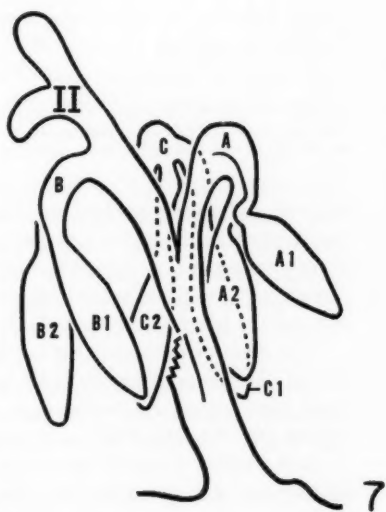
The sporangia were cylindrical sacs 2.0–2.7 mm. long and 0.5–0.7 mm. in



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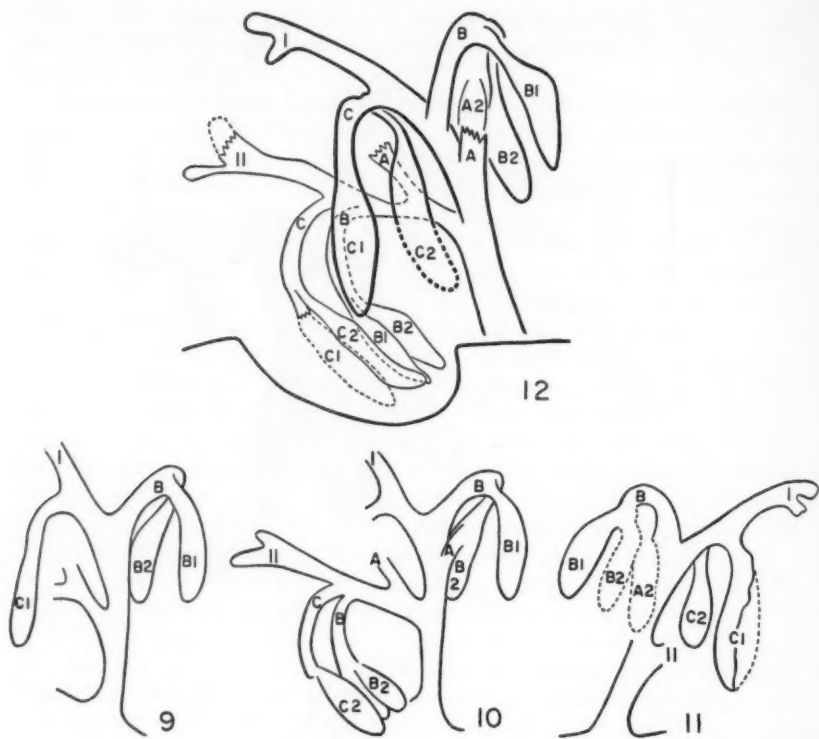


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Text figs. 6-8. 6. Upper segment of sporangiophore (I) shown in figs. 23, 24 (specimen No. 5011/609. 7. Lower segment of same sporangiophore (II); see figs. 25-27. 8. Restoration of same sporangiophore. Arrow points toward apex of specimen as a whole.



Text figs. 9, 10. Stages in the excavation of a sporangiophore of specimen No. 5011/609; see also fig. 31. Text fig. 11. Counterpart of same appendage; see also fig. 30. Text fig. 12. Semi-restoration of same sporangiophore. Detailed explanation in text.

diameter and pointed at the distal end. They were apparently strongly constructed for despite the entangled position in which they occur they are often neither broken nor opened. It is possible that the wall of the sporangium was rather thick, perhaps as a result of several layers of cells or having been fossilized when immature; the latter seems most likely.

The mode of dehiscence has not been positively ascertained. Careful examination of the sporangia on the holotype specimen (No. 5011/609) has revealed no distal pore but on a few sporangia a median longitudinal line is found on the ventral side (fig. 28) which may represent the place of dehiscence.

It is evident from the numerous sporangiophores we have studied that their organization was essentially the same throughout; there are, however, some slight variations and in view of the rather surprising complexity of the fertile appendages as contrasted with previous accounts of Calamophytos it seems pertinent to supplement the description given above with somewhat briefer considerations of several other examples.

Text figure 9 is a camera lucida drawing of an appendage (No. 5011/609) prior to any treatment. The sporangiophore stalk divides into the two divisions; a considerable part of I is present but only the basal part of II. Referring to segment I, branch B is shown with its two sporangia B1 and B2 and one sporangium of the C branch is present. In order to expose segment II, which appeared to dip down into the rock, sporangium C1 was degaged away; after working through the sediment underneath sporangium C1 the II segment was revealed as shown in text fig. 10 and fig. 31. Three branches (A, B and C) were found departing from segment II. Branch C terminates in a single sporangium, C1, but judging from its mode of attachment this is one of an original pair; branch B is terminated by one clearly defined sporangium (B2) and there appears to be another beneath it; the third branch (A) could not be followed.

Text figure 11 and fig. 30 show the counterpart of the appendage; only segment I is present. The sporangia B1, B2 and C1 are readily correlated with their position as shown on the other face of the specimen (text fig. 9); there is some question as to the sporangium labeled A1 and a fifth one appears to the right of sporangium B2 whose position on the segment is undetermined.

Text figure 12 brings this information together as a semi-restoration. It may be noted that there were not less than eight sporangia borne by the entire appendage and the number was probably closer to ten or twelve.

SPECIMEN NO. 5012/337

Some significant information was obtained from this specimen (fig. 1) concerning the general branching pattern of the fertile appendages but, as noted above, very few sporangia could be identified intact due to the fact that dehiscence had apparently taken place some time prior to fossilization. It should be noted that there is no counterpart of this specimen; when it was found during the quarrying operations an extended search was conducted for the other side but it was apparently completely shattered and lost.

The three sketches shown in text figs. 13-15 show an appendage before and after degagement, and a semi-restoration respectively. The initial appearance was essentially as shown in text figure 13 aside from a slight amount of degagement that was necessary to expose branches B and C. The segment was then degaged away, starting at the distal end and extending down to the point indicated by line ---o. The underlying segment (II) was then detected and when completely excavated it appeared as shown in text fig. 14.

The semi-restoration of this appendage (text fig. 15) thus shows it as consisting of two main branches, I and II; II produces at least two secondary branches and terminates in a forked tip; I produces three secondary branches. All of the sporangia had been shed prior to fossilization.

A second example (fig. 6 and text fig. 16) is included since it gives some interesting information concerning the variation in the general morphology of the fertile appendages and particularly the ultimate terminations. It is virtually certain that the upper portion was attached as indicated by the dotted line but this was not positively demonstrated. The essential features of this appendage

seem to be as follows: the main stalk branches into two segments which in turn divide, each giving off several side branches, and terminate in unforked distal tips.

Although specimen No. 5012/337 is the largest one in the collections and the most completely preserved, with reference to the main branch system as a whole, none of the ultimate terminations of the branches are preserved; these probably extended out at least 10 or 15 cm. beyond what is shown in the photo (fig. 1). The ultimate appendages, both sterile and fertile, are for the most part rather poorly preserved and we interpret it as a plant, or portion of a plant, that had shed its spores and undergone partial decay prior to fossilization. Several fertile appendages are sufficiently well preserved as to offer evidence of their relationship with the new species *C. bicephalum*.

DIAGNOSIS

Calamophyton bicephalum Leclercq and Andrews, sp. nov.

Plants consist of a main stem, the basal portion of which is unknown, which divides in a digitate fashion into two to several branches; these branches in turn divide in more or less equal dichotomies. Transverse striations are occasionally present on the main stem and lower portions of the primary branches. The shoot system, above the main axis, appears to be predominantly fertile or sterile. The sterile appendages (leaves) are somewhat more robust on the main stem than above, with a single vascular bundle, and dichotomize one to four times in a three-dimensional pattern and attain a length of about one cm. Fertile appendages are aggregated to form a specialized branch but not in definite cones; a fertile appendage consisted of a basal stalk which divided into an upper and lower segment; each segment bore three short side branches which terminate in a slight bifurcation with a pendulous sporangium attached to each, resulting in a total of twelve sporangia; each of the two main segments terminates in a short dichotomy. Sporangia are cylindrical, pointed at the distal end, 2.0–2.7 mm. long by 0.5–0.7 mm. in diameter, with possibly a line of dehiscence on the ventral side.

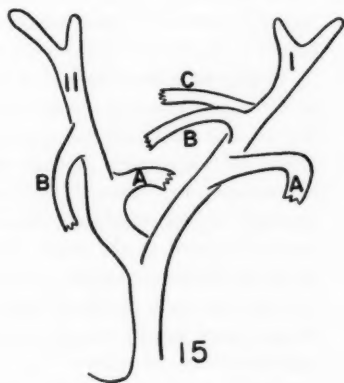
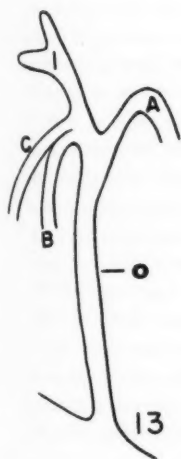
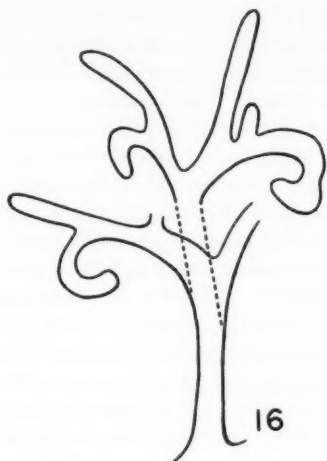
Holotype: No. 5011/609. *Paratypes*: No. 5012/337, No. 5009/588. All preserved in the Laboratoire de Paléontologie Végétale, Université de Liège.

Horizon: lower Givetian, Middle Devonian.

Locality: Carrières Brandt (north quarry), Goé, Belgium.

DISCUSSION

With the exception of the general organization of the branch system the new species of *Calamophyton* described here presents characters, particularly in the nature of the ultimate fertile and sterile appendages, that are quite new. In these features our plant differs sharply from *Calamophyton* as portrayed in all recent text-books. It was quite surprising to find these appendages so complex and it might be supposed that we are actually dealing with plants that should not be identified with this genus. Yet it may be noted that our specimens showed, on the initial split of the rock, rudimentary leaf-like organs (sterile appendages) which are small and once or twice divided apparently in one plane as previously



Text figs. 13-16. 13. A fertile appendage from specimen No. 5012/337 as it appeared originally. 14. Same appendage with segment I removed and underlying segment (II) revealed. Appendage I was formerly attached at break indicated by line ---o. 15. Partial restoration of same appendage. 16. Another appendage from specimen No. 5012/337. Detailed explanation in text.

described for *C. primaevum*. The same holds true for the sporangiophore; for example, these structures give the impression before degagement (figs. 22, 23) of being once forked and in only one plane. This aspect is apparently very similar to the sporangiophore of *C. renieri* (Leclercq, 1940) with the difference that the

small axis of the sporangiophore of *C. bicephalum* is prolonged as an erect appendage. Thus, in order to determine whether *C. primaevum* K. and W. actually had three dimensional leaves a specimen of this species (figs. 17, 18) formerly described by Aderca (1932) was selected for re-investigation.

Figure 15 shows two leaves that were selected as they appeared initially; both dichotomize and of the two resultant branches the left one in both undergoes another forking and, in the case of the lower leaf the left fork is again apically notched. Beginning at their apical extremities the two leaves were degaged away down to the point indicated by the lines 0----0, at which point a branch was found dipping down into the rock matrix. When completely exposed these underlying branches appeared as shown in figure 16 distal to the line 0----0. The latter were thus directly beneath the branches shown in figure 15 and in both leaves the second dichotomy was at right angles to the first; these leaves are shown restored in text figure 5. Thus, in view of the identical morphology found in *C. bicephalum* we consider the three dimensional branching to have generic value.

The prominent characters of *C. bicephalum* are the three dimensional sterile and fertile appendages. The former was a fairly rigid, terete structure with somewhat varied form; wedge-shaped ones, notched at their apex, were found along the lower portions of the primary branches. Higher up the branching of the leaf became more pronounced until the "mature" stage, characterized by four orders of branching, was attained. Attention may be called to the fact that such mature leaves were found on the lower portion of the primary branches of fertile twigs.

It may next be of interest to consider the possible homology of the sterile and fertile appendages. In 1936, Eames noted that "from the evidence provided by *Hyenia* and *Calamophyton* it is apparent that 'leaves' and the fertile tips in this group are homologous". Our study indicated that this is undoubtedly true if one compares a "mature" leaf with a sporangiophore. The latter divides into two main branches, referred to previously as superior and inferior segments, which may correspond to the initial dichotomy of the sterile appendage. Beyond this point the fertile appendage is more complex in that each segment produces three side branches each of which bears a pair of sporangia while the segment proper is elongate and usually terminates in a forked apex. Whether or not the sterile appendages may be termed "leaves" is perhaps a matter of opinion but there would seem to be no doubt that they functioned as such.

The present study is an initial one dealing with the fossil plants from the Goé locality. The difficulty of working with Devonian plants is emphasized by this investigation but in no less degree it is demonstrated that reliable information may be obtained from such ancient land plants when they are well preserved.

It seems pertinent to add a few comments concerning previous work with both *Hyenia* and *Calamophyton* since they are undoubtedly closely related. Of the several species of these two genera that have been described to date none is known in its entirety.

The problem of making significant comparisons with previously described species is rendered difficult by the fact that during the recent war the material

described by Kräusel and Weyland (1926, 1929, 1932) was destroyed although two fragments of the fertile branch system of *C. primaevum*, from Dr. Kräusel's collections, are preserved in the Department of Geology of the University of Cologne. The two fragments on which *C. renieri* (Leclercq, 1940) is based are preserved at the University of Liège. In the light of what has now been found in *C. bicephalum* it may be desirable to rework, with the degaging technique, the available material of the two other species to try to determine the real value of the three specific epithets. It is, however, questionable whether the remaining specimens of the earlier described species are sufficiently well preserved to allow effective comparison, consequently our only course seemed to be to assign a new specific name to the Goé specimens.

In the light of what is now known it seems safe to assert that the only dependable difference between *Hyenia* and *Calamophyton* lies in the general habit of the two. Even this is complicated by the fact that we do not know anything about the basal part of the shoot system of *Calamophyton*. Our specimens do, however, suggest a habit that may be worth a few words of speculation. It seems likely that *C. bicephalum* consisted of upright shoots that were predominantly fertile (fig. 21) or sterile (fig. 7, lower right). If this was the case it seems unlikely that the fertile shoots would have had sufficient photosynthetic tissue to have maintained themselves independently. In explanation it may be supposed that both were borne either on a common erect small "trunk" that would have given the plant a shrub-like appearance, or they were borne on a common rhizome with a relationship comparable to that found in the modern *Equisetum arvense*. It is expected that further studies of the Goé fossils will contribute toward solving this and other problems relating to both *Calamophyton* and *Hyenia*.

SUMMARY

The material on which this study is based came from the lower Givetian (Middle Devonian) of Belgium.

A new species, *Calamophyton bicephalum* Leclercq and Andrews, is created in view of the complexity of the fertile appendages which contrast with homologous structures in the previously described species *C. primaevum* Kräusel and Weyland and *C. renieri* Leclercq.

The investigation has dealt chiefly in elucidating the structure of the sterile and fertile appendages.

The sterile appendages (leaves) are shown to be three dimensional organs that forked once (young leaves) to four times (mature leaves) and were probably rather rigid and terete in cross section. The three dimensional structure of these appendages is considered to have generic value.

The fertile appendage branched into upper and lower segments; each was erect and supported three curved side stalks attached at slightly different levels; each of these stalks terminated in a pair of pendulous sporangia. Thus the entire appendage bore twelve sporangia when all developed. The sporangia were cylindrical and pointed at the distal end, with possibly a line of dehiscence in the ventral side.

ACKNOWLEDGEMENTS

Je désire exprimer ma gratitude au Fonds National de la Recherche Scientifique de Belgique pour les deux campagnes de fouilles qu'il a subsidiées en 1949 et 1952 et au cours desquelles j'ai récolté le matériel ici étudié.

Je remercie le Patrimoine de l'Université de Liège qui m'a permis de recevoir le Professeur Henry Andrews pendant quatre mois à mon laboratoire.

A Monsieur J. DAMBLON vont mes sincères remerciements pour l'attention et le soin avec lesquels il a exécuté la reconstitution du sporangiophore représenté figure 8 du texte.

Je suis particulièrement reconnaissante à Monsieur José LEWALLE, Assistant, et à Monsieur Maurice DISCRY, Préparateur-technicien, de l'aide continue qu'ils ont apportée à l'exécution des nombreux documents photographiques nécessités par cette étude. (Professeur S. LECLERCQ)

This investigation was carried out during my tenure as a Fellow of the John Simon Guggenheim Memorial Foundation; thanks are also due the National Science Foundation for aid in defraying publication costs and in other ways. (HNA)

LITERATURE CITED

- Aderca, B. 1932. Contribution à la connaissance de la flore devonienne belge. *Ann. Soc. Geol. Belgique*, 55:1-16.
- Arnold, C. A. 1947. An introduction to paleobotany. New York, pp. 1-433.
- Eames, A. J. 1936. Morphology of vascular plants, lower groups. New York, pp. 1-433.
- Hirmer, M. 1927. *Handbuch der Paläobotanik*. Munich, pp. 1-708.
- Höeg, O. A. 1945. Contributions to the Devonian flora of western Norway. III. *Norsk Geol. Tidsskrift*, 25:183-192.
- Kräusel, R. and H. Weyland, 1926. Beiträge zur Kenntnis der Devonflora. II. *Senckenberg. naturf. Gesell. Abh.* 40:115-155.
- . 1929. Beiträge zur Kenntnis der Devonflora. III. *Senckenberg. naturf. Gesell. Abh.*, 41:315-360.
- . 1932. Pflanzenreste aus dem Devon. III. Über Hyenia Nath. *Senckenbergiana*, 14: 274-280.
- Leclercq, S. 1940. Contribution à l'étude de la flore du Devonien de Belgique. *Acad. Roy. Belgique Mem.* 12 (fasc. 3):1-65.
- . 1957. Étude d'une fructification de Sphenopside à structure conservée du Devonien Supérieur. *Acad. Roy. Belgique, Classe Sci., Mem.* 4, 14 (fasc. 3):
- Liegeois, R. 1956. Excursion dans le Mesodevonien de l'Est du Synclinorium de Dinant et du Massif de la Vesdre. *Ann. Soc. Geol. de Belgique*, 80:B95-127.
- Magdefrau, K. 1956. *Paläobiologie der Pflanzen*. Jena, pp. 1-443.
- Smith, G. M. 1955. *Cryptogamic botany*. Vol. II. Bryophytes and Pteridophytes. New York, pp. 1-399.
- Walton, J. 1953. An introduction to the study of fossil plants. London, pp. 1-201.

EXPLANATION OF PLATE

PLATE I

Calamophyton bicephalum Leclercq and Andrews
Figures 1-6: specimen No. 5012/337

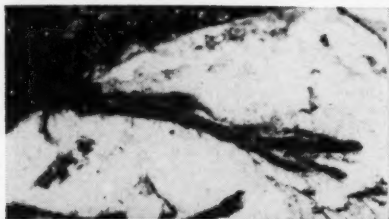
Fig. 1. A large specimen shown natural size. Figs. 2-5. Sterile appendages taken from points a-d, respectively, on specimen shown in fig. 1; all magnified $\times 5$. Fig. 6. A partially preserved fertile appendage; see also text fig. 16 and description in text (p. 14); magnified $\times 5$.



LECLERCQ & ANDREWS—*CALAMOPHYTON BICEPHALUM*



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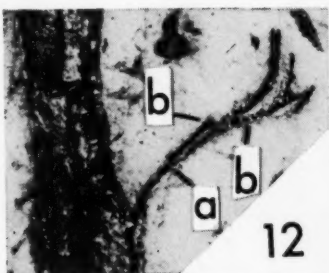
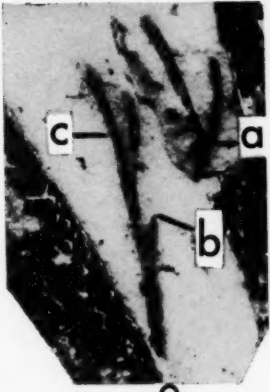


EXPLANATION OF PLATE

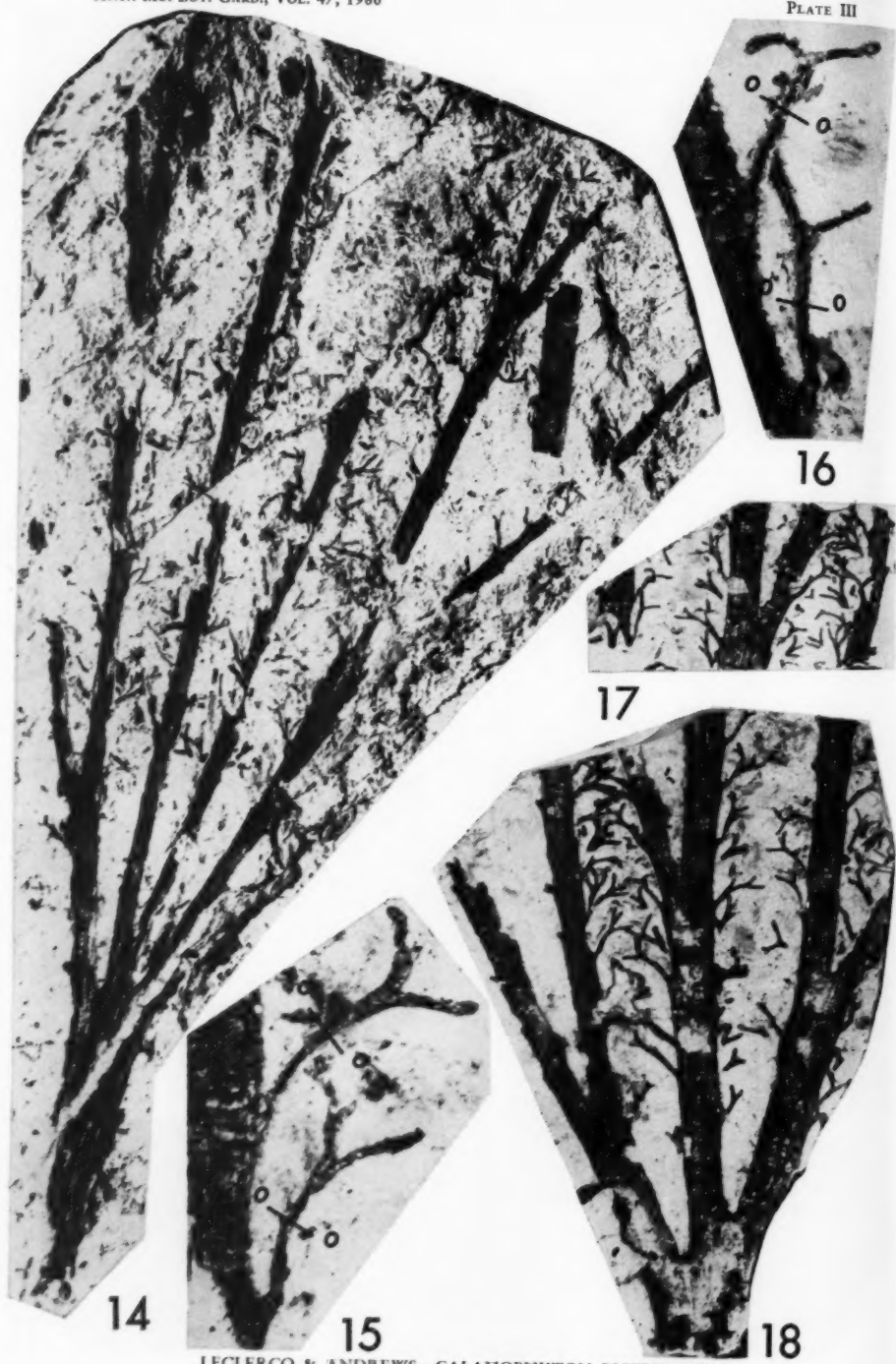
PLATE II

Calamophyton bicephalum Leclercq and Andrews
Figures 7-13: specimen No. 5009/588

Fig. 7. Two specimens shown natural size. Fig. 8. Leaf taken from point *b* in fig. 7; $\times 5$. Fig. 9. Leaf showing four orders of branching; $\times 5$. Fig. 10. Portion of vascular strand from leaf shown in fig. 11; $\times 62$. Fig. 11. Leaf with vascular strand preserved from point *a* in fig. 7; $\times 3$. Fig. 12. Leaf from point *c* in fig. 7; $\times 5$. Fig. 13. Leaf showing four orders of branching from point *d* in fig. 7; $\times 5$.



LECLERCQ & ANDREWS—CALAMOPHYTON BICEPHALUM



LECLERCQ & ANDREWS—*CALAMOPHYTON BICEPHALUM*

EXPLANATION OF PLATE

PLATE III

Calamophyton bicephalum Leclercq and Andrews

Fig. 14. Specimen No. 5007/346. $\times 1$.

Calamophyton primaevum Kräusel and Weyland

Fig. 15. Two leaves from specimen No. 5006, $\times 5$, shown as they appeared originally. Fig. 16. Same leaves as in fig. 15 after degagement; portions distal to lines o---o were revealed after corresponding parts in fig. 15 were degaged away. These two leaves are shown on the right side of the extreme left branch of fig. 17. Fig. 17. Portion of specimen No. 5006, $\times 1$. Fig. 18. Counterpart of specimen No. 5006, $\times 1$.

EXPLANATION OF PLATE

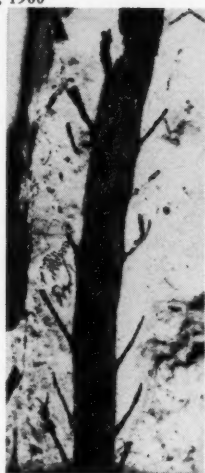
PLATE IV

Calamophyton bicephalum Leclercq and Andrews

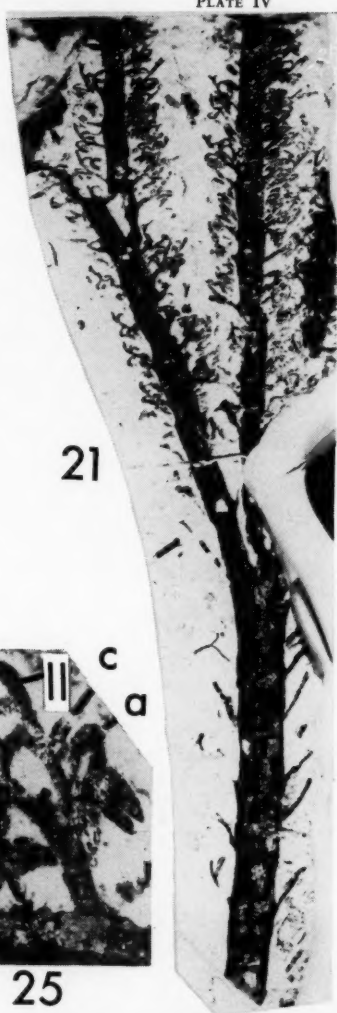
Fig. 19. Leaf showing four orders of branching from specimen No. 5009/588, $\times 5$.
Fig. 20. Main stem of specimen No. 5011/609, $\times 1$. Fig. 21. Holotype specimen No. 5011/609 shown natural size; figure 20 is counterpart of main stem shown here. Figs. 22-27 show stages in the excavation of a fertile appendage from specimen No. 5011/609; for explanation see text (p. 10); all $\times 5$. Fig. 28. Portion of fertile appendage from specimen No. 5011/609, $\times 5$.



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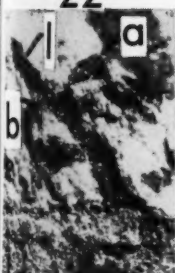
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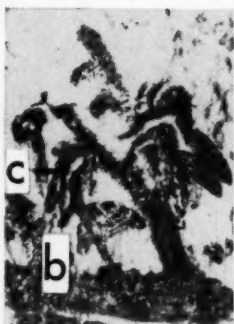
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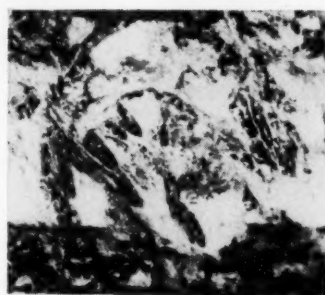
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LECLERCQ & ANDREWS—*CALAMOPHYTON BICEPHALUM*

EXPLANATION OF PLATE

PLATE V

Calamophyton bicephalum Leclercq and Andrews

Fig. 29. Upper portion of holotype specimen No. 5011/609 (as shown in fig. 21) enlarged three times. Figs. 30, 31. Part and counterpart of a fertile appendage from specimen No. 5011/609, $\times 5$; see also text figures 9-12 and description in text (p. 13).

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CLASSIFICATION AND PHYLOGENY IN THE ORCHIDACEAE

ROBERT L. DRESSLER AND CALAWAY H. DODSON

ABSTRACT

The nomenclature of tribes and subtribes in the Orchidaceae is reviewed, and brought into line with the rules of botanical nomenclature. Tribal definition is discussed, and a different delineation of the Neottieae and Epidendreae is proposed. The Apostasiae are considered to be primitive orchids. The Vandae are not considered to be clearly separable from the Epidendreae. A "phylogenetic" arrangement of recognized subtribes is proposed, and keys are given. A broader interpretation is given, especially of the subtribes Chloraeinae, Spiranthinae, Cyrtopodiinae, Epidendrinae, Maxillariinae and Oncidiinae. About 40 subtribes are recognized (as compared to 80 in Schlechter's system). The need for further revision is recognized. Evolutionary patterns are discussed for several features of the orchid plant, and the phylogeny of the family briefly considered. ROBERT L. DRESSLER, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri; CALAWAY H. DODSON, Instituto Botánico, Universidad de Guayaquil, Guayaquil, Ecuador.

INTRODUCTION

The Orchidaceae form one of the largest families of angiosperms, as well as one of the most fascinating by reason of their diversity and specialization in floral structure. A satisfactory classification of the orchids into tribes and subtribes is not yet available. The most commonly used system, that of Schlechter, has for some time not been in accord with the rules of nomenclature, and has many features which may be questioned on botanical grounds. The recent International Botanical Congress has clarified the rules concerning the nomenclature of categories between family and genus, and provides an occasion for a reevaluation of nomenclature in the Orchidaceae. In reviewing the groups within the Orchidaceae we have, of necessity, made a number of observations on relationships and probable phylogeny within the family. These form the final portion of this paper.

While many workers have described new genera and species of orchids, there has been very little monographic work, and we may safely say that the family has really been very little studied, considering its size and complexity. Until there has been a great deal more systematic study of the family it will not be possible to present a finished system of tribes and subtribes. Consequently, no new taxa are presented in this paper, but we have attempted only to review and evaluate previous systems of classification, and to present a tentative system, with synonymy.

Swartz, in 1880, first divided the orchids into those with a single fertile anther and those with two fertile anthers, thus providing the basis for the subfamilial divisions now recognized. Lindley, in his "Orchidearum sceletos" (1827), was the first to divide the family into tribes. In this work he recognized eight tribes. Later, in "The Genera and Species of Orchidaceous plants," only seven tribes were maintained, with "sections" or "divisions" recognized under some of these. Reichenbach never presented a detailed system of orchid classification, and his categories were vague and inconsistent in both rank and spelling (1852, 1884). Bentham (1881), in preparing a system for *Genera Plantarum*, recognized only five tribes, and delineated 27 subtribes under these. Pfitzer (1887) criticized the classification of Bentham and offered a revised system, based primarily on vegetative features. While the rank of Pfitzer's categories was not very clearly indicated,

one finds that the groups with names ending in "-inae" are referred to as "Tribus." Thus Pfitzer's classification recognized 32 tribes, with a number of subtribes. This same system was followed in "Die Natürlichen Pflanzenfamilien," with only minor changes. Pfitzer's classification was the basis for Schlechter's posthumously published "System der Orchidaceen" (1926). Schlechter, however, recognized only four tribes and treated the remaining tribes and subtribes of Pfitzer all as subtribes, of which he enumerated eighty. Some of Schlechter's subtribes were characterized in earlier papers (1911, 1915) as "Gruppen," but only in the 1926 paper were they treated as subtribes. In studying Schlechter's work, one often feels that his system was published in unfinished form, and that he might have presented a much more coherent system, had he lived to complete it. Mansfeld (1937) has reviewed Schlechter's system and made some modifications, but most recent authors have followed Schlechter's original system with little change. Recently Hawkes and Heller (1959) have presented a list of subtribes and genera in which they recognize no less than 88 subtribes.

Schlechter might well be characterized as a "splitter"; he followed very narrow concepts at all levels of his classification. Subsequent workers have reduced a large proportion of his genera and species to synonymy, but most have accepted his tribes and subtribes with little question. Actually, many of the subtribal boundaries drawn by Schlechter have proven to separate closely related genera. In several cases genera assigned to different subtribes have proven interfertile. While Schlechter recognized eighty subtribes in the subfamily Orchidoideae and several others have since been proposed, we tentatively recognize only about forty in our proposed revision. We believe that future study may further reduce the number of subtribes to be recognized. While the rules of nomenclature permit an almost excessive number of categories between genus and species (subgenus, section, subsection, series and subseries), there are relatively few categories between family and genus. Where Schlechter's subtribes seem useful, even though too closely related or too poorly defined, we have indicated them as "alliances." These are not intended to have formal nomenclatural status. To recognize them as subtribes would tend too much toward taxonomic inflation, and would tend to obscure the really close relationships which exist within the family.

Some authors have cast doubt on the validity of genera which are interfertile. While we do not believe that a fertility criterion (alone) can be applied for generic status in the orchids, we do feel that interfertile genera should not be placed in separate subtribes. In every case where authentic hybrids have been reported between subtribes, however, the morphological evidence, alone, favors their union into a single group. In those cases where we feel quite sure that closely related genera were separated in Schlechter's system, we have united them into a single subtribe. In other cases, however, we have deferred judgment because of insufficient familiarity with the plants involved.

The main difference between Schlechter's system and our own is that he emphasized differences, while we are seeking resemblances. His system was primarily analytical and aimed at identification (though often faulty for that purpose), while our own is synthetic, as we believe these higher categories should be. This

is not to belittle the key features used by Schlechter. Where valid, these are still available for keying groups within the subtribes, but relationships are, we hope, more clearly shown in our system. In many cases the key features chosen by Schlechter will separate only a portion of the genera in closely related or artificial groups.

There are primarily three features of the International Code of Botanical Nomenclature which affect the choice or form of names used in this paper. In the case of subfamilies, tribes or subtribes, the name of any taxon which includes the type of the next higher taxon must be based on the same stem as the name of the next higher taxon. Thus "Ophrydeae" and "Platantherinae," for example, must be replaced by Orchidoideae and Orchidinae, respectively. This requirement, which was only recently added to the rules (by the 1959 Congress) causes a few changes, but should cause no confusion, and in general makes the taxonomy at this level more logical. The requirement of the suffixes *-oideae*, *-ae* and *-inae* for subfamilies, tribes and subtribes has been in the rules for some time, but has often been ignored by those dealing with orchid nomenclature. The same is true of the principle of priority, which demands the use of names proposed by Bentham, where these differ from those used by later workers.

TRIBAL DELINEATION

The separation and characterization of the tribes Apostasiae and Cypripediae is relatively clear. Each forms a distinctive and natural group which is easily recognized. In the subfamily Orchidoideae the situation is rather different. The tribe Orchidoideae is distinctive and rather easily characterized, though clearly related to the Neottieae. The distinction of further tribes is much less clear. In Schlechter's system all of the genera with mealy or sectile pollen (except the Orchidoideae) are grouped in the tribe Polychondreae (= Neottieae), while the genera with hard, waxy pollinia are separated as the more advanced tribe Kerosphaerae (= Epidendreae). As Mansfeld has shown, the distinction between mealy and waxy pollinia is neither practical nor natural. Some genera of the Bletinae have, according to Mansfeld, mealy pollinia. Certainly most of the remaining genera have rather soft pollinia. Some genera of the Sobraliinae have hard pollinia and this subtribe shows close affinity to the Thuniinae and the Epidendrinae. Similarly, the Arethusinae have mealy pollinia, but *Crybe* and *Jimensia* (*Bletilla*) are closely related to *Bletia*. There is a complete series ranging from free pollen grains to the hard ceraceous pollinia of the Oncidiinae and Sarcanthinae. Any arbitrary degree of cohesion chosen as a dividing line would split natural genera and subtribes. Mansfeld (1937) placed the Arethusinae and Sobraliinae in the Epidendreae, and this action is supported by the morphological studies of Hirmer (1920). Such a system, though, leaves no practical way of distinguishing the Epidendreae and Neottieae and is, we believe, still unnatural. The subtribes Vanillinae, Pogoniinae and Gastrodiinae seem to show much closer relationship to the Sobraliinae and Arethusinae than to the other subtribes of the Neottieae. By placing these subtribes in the Epidendreae one achieves a system which is both

more natural and more practical. By this arrangement the great majority of the primitive Epidendreae (with mealy pollinia) have incumbent, operculate anthers, like those of *Phajus* or *Cattleya* (see fig. 3D). The position of the anther in the more advanced Epidendreae is extremely diverse, but these are easily distinguished by the truly hard pollinia. A few species of primitive Epidendreae, such as *Triphora* and some species of *Epistephium* and *Elleanthus*, have erect anthers. Thus the position of the anther is not a fool-proof key feature, but it does seem to provide a better practical separation, as well as a more natural classification.

Several authors have distinguished the tribes Epidendreae and Vandeeae on the basis of pollinia structure, but a clear distinction proves to be difficult. The presence or absence of a stipe is one feature which has been used for this purpose, but some genera which would unquestionably belong in the "Vandeeae" have little or no stipe, while a few other genera which are not closely related have stipes or stipe-like structures (Genyorchidinae, Thecostelinae, some species of *Polystachya*). Another feature which is characteristic of the "Vandeeae" is the presence of superposed pollinia; yet *Coelogyne* and some species of *Thuniinae* and *Polystachya* have more or less superposed pollinia, but seem otherwise not referable to the "Vandeeae." There seems to be no feature or combination of features which will serve to separate the more advanced Orchidoideae into two clear-cut main groups. There is a general trend from plants with terminal inflorescence and relatively simple pollinia to those with a lateral inflorescence and highly specialized pollinia, but there is no sharp break and the relationships seem too reticulate to admit the separation of two tribes on this basis. The subtribes of the "Vandeeae" (Cyrtopodiinae to Oncidiinae as listed on p. 29) seem to represent a relatively homogeneous and more specialized offshoot from some of the several evolutionary lines within the remainder of the Epidendreae. All of these subtribes appear to have been derived from more or less *Eulophia*-like ancestors. For this reason, it is sometimes convenient to consider them as a unit, and a better understanding of the subtribes related to the Cyrtopodiinae may indicate a sharper break between the two main divisions of the Epidendreae than is now evident.

While the Epidendreae form a natural and closely knit group, the Neottieae are more diverse in terms of relationship. Even with the removal of the Vanillinae, Pogoniinae and Gastrodiinae, it is not certain that the Neottieae form a really natural group. Including all of these genera in one tribe because they all possess mealy pollen is somewhat comparable to a hypothetical grouping of *Vanilla*, *Selenipedium*, and *Apostasia* into a single taxon because of seed characteristics. Mealy pollen, like the sclerotic seed coat and the lateral anthers of the Cyripedioideae, is a feature which was doubtless found in all orchids at an early stage in orchid evolution. Its occurrence in two or more otherwise dissimilar groups is scarcely strong evidence of relationship. Since the present paper is primarily a review of orchid classification, any major reorganization of the Neottieae or the Cyripedioideae must be deferred for the present. The possible groupings within these taxa are discussed in the final section on tribal phylogeny (p. 62).

Subfamily Cyripedioideae

Tribe 1. Apostasiae

Tribe 2. Cyripedieae

Subfamily Orchidoideae

Tribe 3. Neottieae

Subtribe Limodorinae

Chloraeinae

Rhizanthellinae

Pterostylidinae

Neottiinae

Diuridinae

Cryptostylidinae

Prasophyllinae

Spiranthinae

a. *Tropidia* allianceb. *Goodyera* alliancec. *Spiranthes* allianced. *Cranichis* alliance

Tribe 4. Orchideae

Subtribe Epipogiinae

Orchidinae

Disinae

a. *Disa* allianceb. *Satyrium* alliance

Coryciinae

Tribe 5. Epidendreae

Subtribe Vanillinae

Gastrodiinae

Pogoniinae

Sobraliinae

Thuniinae

Arethusinae

Bletiinae

Collabiinae

Tribe 5. Epidendreae (Continued)

Subtribe Coelogyninae

Epidendrinae

a. *Epidendrum* allianceb. *Eria* alliancec. *Polystachya* allianced. *Glomera* alliancee. *Podochilus* alliancef. *Arpophyllum* alliance

Pleurothallidinae

Adrorhizinae

Thelasiinae

Ridleyellinae

Liparidinae

Dendrobiinae

Genyorchidinae

Thecostelinae

Cyrtopodiinae

Catasetinae

Cymbidiinae

Sarcanthinae

Stanhopeinae

Maxillariinae

a. *Zygopetalum* allianceb. *Lycaste* alliancec. *Maxillaria* alliance

Pachyphyllinae

Cryptocentrinae

Oncidiinae

a. *Oncidium* allianceb. *Ornithocephalus* alliancec. *Dichaea* alliance

Subtribes of uncertain position

Grobyinae

Pachyplectrinae

A PROPOSED PHYLOGENETIC LIST OF SUBTRIBES

Above is given a list of the tribes and subtribes which we recognize, followed by a tentative key to tribes. We have, in nearly all cases, changed the endings of the group names to accord with the rules of nomenclature. Very few of them were published in the appropriate form, though status was clearly indicated. We have attempted to arrange the groups in a "phylogenetic" sequence; that is, we

have tried to place the more primitive members at the beginning of each group, and we have tried to place closely allied groups together, where possible. The limitations of a one-dimensional scheme are obvious; there are, for example, a number of subtribes which should be immediately adjacent to the Epidendrinae in any "natural" system, but only two can be so placed. We have indicated groups of related subtribes by lines, but interrelationships within the Epidendreae are better shown in figure 1 (p. 51).

KEYS

As Schweinfurth has indicated (1959, p. 528), orchid identification has continued to be more of an art than a science. This is, in part, due to continued reliance on unworkable keys. Since previously published keys to the Orchidaceae have proven to be inadequate in many features, we have prepared these keys *de novo*, as much as possible. Comparison will show Schlechter's key to be much simpler in many respects. To this we can only reply, "Yes, but his key doesn't work." There will surely be many sections in these keys where a similar complaint is justified. It is extremely difficult to write a workable key to the orchids of the world. The person working in a single continent has an easier time of it, and would do well to prepare his keys independently, rather than trying to adapt either these or Schlechter's keys. An English translation of Schlechter's key, with some revision, is given in Withner's recent book (Schweinfurth, 1959).

KEY TO SUBFAMILIES AND TRIBES

1. Fertile anthers 2 or 3; filaments more or less united to the style, but arising below the level of the stigma; the stigma and terminal portion of the style free; no rostellum present.....subfamily CYPRIPEIDIOIDEAE.....2
1. Fertile anther 1 (or 3 as an abnormality and in some autogamous forms); filaments united with the style to form a distinct column, united for the full length of the style or the anther and stigma connected by a terminal rostellum.....subfamily ORCHIDOIDEAE.....3
- 2(1). Perianth essentially regular, the lip never deeply saccate; fertile anthers 2 or 3, elongate; style slender.....APOSTASIEAE
2. Perianth irregular, with a deeply saccate lip; fertile anthers 2, subglobose; a conspicuous, flattened median staminode present; style relatively thick.....CYPRIPEIDAE
- 3(1). Pollinia 2 to 8, hard, waxy; anther usually caducous; leaves various, often articulate; habit of growth various.....EPIDENDREAE
3. Pollinia 2 or 4, soft, mealy, in tetrads or granular masses; anther persistent or deciduous; leaves usually herbaceous, not articulate; growth usually sympodial with a terminal inflorescence.....4
- 4(3). Anther erect or reclinate (rarely incumbent), persistent, usually broadly joined to the column; pollinia in soft masses (sectile), caudicles arising from the base of the pollinia.....ORCHIDEAE
4. Anther erect or incumbent, narrowly joined to the column, commonly caducous or withering; pollinia mealy or sectile, without caudicles or these indistinct and terminal.....5
- 5(4). Anther terminal and operculate (incumbent) or rarely erect, usually more or less versatile; stems often with corms or corm-like thickenings.....EPIDENDREAE
5. Anther more or less erect, often dorsal (terminal and operculate in some species of *Acianthus*); stems without corms or other thickenings.....NEOTTIEAE

SYNONYMY AND DISCUSSION

In the following section we give keys to subtribes and list the subtribes alpha-

betically under the tribes, with synonymy and discussion where appropriate. We have not given full citations with the names of tribes and subtribes, but the papers containing new tribes or subtribes are indicated by an asterisk in the bibliography. We estimate that there are about 600 distinct, valid genera in the Orchidaceae. A really critical enumeration of genera is not yet possible. The lists given here are based primarily on Schlechter (1926), and doubtless contain some genera which do not merit recognition, while omitting others which should be listed. Only for the *Epidendrum* and *Oncidium* alliances can we indicate with some confidence the genera which will be maintained by critical revision; and, even here, there are genera of which we have not yet seen adequate or living material. If these alliances are representative of the family, the total number of valid genera may be well under 600.

Subfamily CYPRIPEIDIOIDEAE Lindley (Diandrae Kunth, Pleonandrae Pfitzer [1903], Apostasioideae Wettstein)

Tribe 1. APOSTASIEAE R. Brown (Pulverae Blume, in part)

Some authors have excluded the Apostasiae as a separate family. We, however, agree with Rolfe (1909), J. J. Smith (1934), Mansfeld (1934) and Holttum (1953), that these plants cannot logically be excluded from the family without also excluding the Cyripedieae, and we feel that neither action is desirable. A classification which excludes the Apostasiae because they are inconspicuous and retains the Cyripedieae because they are showy is scarcely acceptable. It is possible, of course, that detailed study will show the Apostasiae to be basically different from other orchids in some features. As far as present knowledge goes, they are primitive orchids, and quite as closely related to some Neottieae as these are to the other orchids. As Godfery (1932) indicates, there is little evidence of close relationship between the Apostasiae and Cyripedieae, even though they show the same basic plan of flower structure. It is quite possible that the current subfamilial division is artificial.

Apostasia, *Neuwiedia*.

Tribe 2. CYPRIPEIDIEAE

The four genera of ladyslippers form a relatively uniform relic group. They are markedly divergent from most other orchids in that the median anther is represented by a large shield-like staminode. In spite of their differences, the ladyslippers are orchids in good standing. The three abaxial stamens, resupination, reduction in seed structure, mycorrhizal relationship, and the less obvious features which predispose the family to evolution as epiphytes are themes which run throughout the family. The primitive features to be found in *Selenipedium* are strongly reminiscent of those found in other primitive orchids, though they do not, of course, necessarily indicate close relationship. Mansfeld (1937a) notes some resemblances between the Cyripedieae and *Epipactis*.

Cyripedium, *Paphiopedilum*, *Phragmipedium*, *Selenipedium*.

Subfamily ORCHIDOIDEAE (Monandreae Kunth)

Tribe 3. NEOTTIEAE Lindley (Granulosae Blume [in part], Pulverae Blume [in part], Goodyereae King & Pantling, Listereae King & Pantling, Polychondreae Schltr., Epipactieae Hatch [illegitimate, because nomenclaturally superfluous when published])

KEY TO SUBTRIBES

1. Anther more or less terminal, erect or inclined, projecting beyond the stigma or rostellum; viscidium, if present, commonly attaching to the base or ventral surface of the pollinia, rarely to the apex.....2
1. Anther dorsal, not projecting beyond the erect rostellum; pollinia usually attached to a terminal viscidium.....6
- 2(1). Plants subterranean, or the flowers scarcely penetrating the surface of the soil; leafless saprophytes with the flowers in dense bracteate heads (Australia).....RHIZANTHELLINAE
2. Plants appearing above the soil, usually forming leaves.....3
- 3(2). Rostellum sensitive, secreting a viscid drop when touched, or appearing to form a viscidium; small, slender-stemmed plants with 2 sub-opposite cauline leaves (leafless saprophytes in *Neottia*) (north temperate).....NEOTTIINAE
3. Rostellum not sensitive, with or without a viscidium; leaves usually either several or basal.....4
- 4(3). Leaves cauline, spiral (absent in *Limodorum* and *Apbyllorchis*); lip usually divided into a basal, more or less saccate portion and a terminal, often hinged, portion (sub-entire and spurred in *Limodorum*); rostellum present or absent (largely north temperate).....LIMODORINAE
4. Leaves often basal; lip not as above; rostellum usually present.....5
- 5(4). Lip hinged, with a retrorse appendage at the hinge, actively motile (sensitive) (Australasia).....PTEROSTYLIDINAE
5. Lip various, but not actively motile (South America and Australasia).....CHLORAEINAE
- 6(1). Column with distinct lateral wings or staminodia; plants with fascicled roots and basal leaves.....7
6. Column usually without distinct wings or staminodia; habit various.....9
- 7(6). Pollinia with a distinct caudicle-like stipe (Australasia).....PRASOPHYLLINAE
7. Pollinia without a stipe.....8
- 8(7). Staminodia very prominent, scarcely adnate to the style; column not more or less hidden by the enfolding lip base; sepals or petals relatively broad (Australasia).....DIURIDINAE
8. Staminodia relatively small; column very short, nearly hidden by the base of the lip; both sepals and petals very narrow (Australasia).....CRYPTOSTYLIDINAE
- 9(6). Rostellum sensitive, secreting a viscid drop when touched, or appearing to form a viscidium; small, slender-stemmed plants with 2 subopposite cauline leaves (leafless saprophytes in *Neottia*) (north temperate).....NEOTTIINAE
9. Rostellum not sensitive, usually with a distinct viscidium; habit not as above (widespread).....SPIRANTHINAE

CHLORAEINAE Pfitzer (Caladeniinae Pfitzer, Thelymitrinae Pfitzer, Acianthinae Schltr., Corysanthinae Schltr., Megastylidinae Schltr., Corybasinae Mansf. [not validly published, unless later (1954) reference to Corysanthinae Schltr. be taken to validate its publication as a new name. Corysanthinae, however, is a valid name, though based on a synonym])

This is the group which includes most of the bizarre Australian genera. The striking modifications have led to the naming of several subtribes, but these do not seem tenable, at least as previously delimited. *Thelymitra* is distinctive because of its nearly regular perianth, which is frequently blue, but it is closely allied to the

other genera through *Calochilus*, *Adenochilus* and *Glossodia*. Some species of *Thelymitra* are unusual for this group in the attachment of the rostellum or viscidium to the apex of the pollinia, but this is not consistent within the genus. Some species of *Acianthus* are very unusual in the form of the column and the position of the anther (operculate), but *A. reniformis* is more representative of the subtribe in these features; Mansfeld's action in grouping *Acianthus* with *Caladenia*, thus seems correct. *Corybas* is closely related to *Caladenia*. The three American genera *Chloraea*, *Bipinnula* and *Asarca* are somewhat distinctive in habit, but the other American genus, *Codonorchis*, is closely related to both *Chloraea* and *Caladenia*. Most of the Australian genera show a characteristic pitted, conic anther.

Acianthus, *Adenochilus*, *Asarca*, *Bipinnula*, *Burnettia*, *Caladenia*, *Calochilus*, *Chiloglottis*, *Chloraea*, *Codonorchis*, *Corybas*, *Epiblema*, *Eriochilus*, *Glossodia*, *Leptoceras*, *Lyperanthus*, *Megastylis*, *Rimacola*, *Thelymitra*, *Townsonia*.

CRYPTOSTYLIDINAE Schltr.

Cryptostylis is a distinctive genus, though without striking key features. Some species mimic insects and are involved in the strange relationship of pseudocopulation. This subtribe, the Diuridinae and the Prasophyllinae seem to form a distinct group with column structure similar to that of the Spiranthinae. The degree of relationship to the Spiranthinae is uncertain.

Coilochilus, *Cryptostylis*.

DIURIDINAE Benth

This group is of special morphological interest because of the large staminodia and because the filament and style are scarcely united into a column. Some Spiranthinae show similar columnar structure, though without the staminodia.

Diuris, *Orthoceras*.

LIMODORINAE Benth (Cephalantherinae Pfitzer, Epipactiinae Godfrey)

The Limodorinae include genera which are quite primitive in some respects, and, being largely European, they have been studied much more than other primitive orchids.

Aphyllorchis, *Cephalanthera*, *Epipactis*, *Limodorum*.

NEOTTIINAE (Listerinae Schltr.)

These genera are distinctive in the sensitive rostellum, which forcibly extrudes a viscid droplet when touched. The anther is either erect or somewhat incumbent on the subequal rostellum. These genera show some resemblances to the Limodorinae, and, like that group, have relatively large chromosomes (Duncan, 1959).

Listera, *Neottia*.

PRASOPHYLLINAE Schltr.

Mansfeld placed these genera with *Thelymitra*, but they are distinctive in aspect, and unusual in the possession of stipes. These are generally described as

caudicles, but are not derived from the pollinia (see Vermeulen, 1959). This group seems more nearly allied to the Diuridinae and Cryptostylidinae.

Corunastylis, *Goadbyella*, *Microtis*, *Prasophyllum*.

PTEROSTYLIDINAE Pfitzer (Drakaeinae Schltr.)

These Australian genera are remarkable for their sensitive, motile lip, but very closely allied to the Chloraeinae, and especially to *Cbiloglottis*.

Caleana, *Drakaea*, *Pterostylis*, *Spiculaea*.

RHIZANTHELLINAE Rogers

Rogers placed this group near the Gastrodiinae, but the form of the lip, column and anther indicate that they are allied to *Caladenia*.

Cryptanthemis, *Rhizanthella*.

SPIRANTHINAE Bentham (Corymbidinae Bentham [based on *Corymbis*, an orthographic variant of *Corymborchis*], Cranichidinae Pfitzer, Physurinae Pfitzer [based on *Physurus* L. C. Rich., nom. nud.], Tropidiinae Pfitzer, Maniellinae Schltr.)

We feel confident that the Spiranthiniae and Cranichidinae should be merged. These groups have much the same floral structure, and we see little justification for separating them, especially if some American authors are correct in reducing Schlechter's Spiranthiniae nearly to a single genus. The genera included in the *Goodyera* alliance are somewhat distinct in habit (rooting at the nodes, rather than roots fascicled), but agree well in floral features. Here, too, there seem to be too many genera. If future study should indicate the advisability of segregating the group as a separate subtribe, the name might be based on the familiar genus *Goodyera*. The *Tropidia* alliance seems to have the strongest claim to subtribal distinction, but no differences in floral structure have been demonstrated. In habit, these genera resemble *Palmorchis*, of the Sobraliinae, and *Apostasia*. The earliest subtribal name, Corymbidinae, should be changed in form, if it is to be used.

KEY TO ALLIANCES

1. Stem hard, woody; leaves subcoriaceous, strongly plicate, with several prominent nerves beneath (widespread).....*Tropidia* alliance
1. Stem and leaves herbaceous, leaves not strongly plicate.....2
- 2(1). Roots not fascicled, scattered along the stem or rhizome; pollinia often sectile (widespread).....*Goodyera* alliance
2. Roots usually fascicled; pollinia not sectile.....3
- 3(2). Flower resupinate, lip lowermost (widespread, but predominantly American).....*Spiranthes* alliance
3. Flower not resupinate, lip uppermost (American).....*Cranichis* alliance
 - a. GOODYERA ALLIANCE: *Anoectochilus*, *Cheirostylis*, *Cystopus*, *Cystorchis*, *Dicerostylis*, *Dossinia*, *Erythrodes* (*Physurus*), *Eucosia*, *Eurycentrum*, *Gonatostylis*, *Goodyera*, *Gymnochilus*, *Haemaria*, *Herpysma*, *Hetaevia*, *Hylophila*, *Kublbasseltia*, *Lepidogyne*, *Macodes*, *Moerenhoutia*, *Myrmecbis*, *Odontochilus*, *Orchipeidum*, *Papuaea*, *Platylepis*, *Tubilabium*, *Vrydagzynea*, *Zeuxine*.
 - b. CRANICHIS ALLIANCE: *Altensteinia*, *Baskervillea*, *Cranichis*, *Fuertesicella*, *Pontbeiva*, *Porphystachys*, *Prescottia*, *Pseudocentrum*, *Pterichis*, *Solenocentrum*, *Stenoptera*, *Wulfschlaegelia*.

c. SPIRANTHES ALLIANCE: *Centrogenium*, *Eurystyles*, *Lankesterella*, *Manniella*, *Pelexia*, *Sarcoglottis*, *Sawroglossum*, *Spiranthes*.

d. TROPIDIA ALLIANCE: *Corymborchis*, *Tropidia*.

Tribe 4. ORCHIDEAE (Granulosae Blume. [in part], Ophrydeae Lindley, Epipogieae Parlatores)

Here, except for the inclusion of the Epipogiinae in this tribe, we have followed essentially the classification of Bentham, which seems to be the best. There are still several problems in the morphological interpretation of flower structure in the Orchideae. Until this is better understood, it is difficult to consider the evolution or relationships of the group. As Godfery (1933) and Swamy (1949) have indicated, the Orchideae are clearly more highly specialized than the majority of Neottieae, and should not precede them in a phylogenetic scheme.

KEY TO SUBTRIBES

1. Lip erect, adnate to the face of the column, commonly bearing an appendage which overtops the anther; dorsal sepal and petals commonly forming a hood (Old World).....CORYCHINAE
1. Lip free from the column.....2
- 2(1). Leafless saprophytes; the anther erect or incumbent, narrowly attached to the column (Old World).....EPIPOGIINAE
2. Autophytes with green leaves (except for *Silvorchis*); the anther erect or reclinate, broadly attached to the column.....3
- 3(2). Anther erect or suberect, not projecting dorsally from the column; stigma simple or often divided into 2 separate, often stipitate, lobes; spur, if present, single and formed by lip (widespread).....ORCHIDINAE
3. Anther more or less reclinate, projecting dorsally from the column, or recumbent, with the base uppermost, rarely suberect; stigma not divided into two completely separate lobes; median sepal sometimes spurred (Old World, predominantly African).....DISINAE

CORYCHINAE Bentham (Disperidinae Schltr.)

Ceratandra, *Corycium*, *Disperis*, *Pterygodium*.

DISINAE Bentham (Satyriinae Pfitzer)

These genera seem better treated as a single subtribe. The position of the saprophytic *Silvorchis* is uncertain.

KEY TO ALLIANCES

1. Flowers resupinate; spur, when present, formed by median sepal; column relatively short (Africa).....Disa alliance
1. Flowers not resupinate; spur or spurs, when present, formed by lip; column usually elongate (Old World).....Satyrium alliance
- a. DISA ALLIANCE: *Brownleea*, *Disa*, *Schizodium*.
- b. SATYRIUM ALLIANCE: *Pachites*, *Satyrium*, *Silvorchis*?

EPIPOGIINAE Schltr.

Recent authors have placed these genera in the Neottieae, but the persistent anther and the sectile pollinia with basal caudicles indicate a much closer affinity with the Orchideae. Godfery (1933) followed Parlatores (1858) in treating

Epipogium as the type of a separate tribe. In *Epipogium apbyllum* the anther is incumbent and the pollinia are parallel with the caudicles, which attach to a viscidium near the apices of the pollinia. It is not clear that the incumbent anther indicates a relationship with the primitive Epidendreae; the peculiar orientation of the caudicles suggests that it is a derived condition in this species. Rohrbach (1866) gives detailed illustrations of *E. apbyllum*. The anther is erect in the autogamous *E. roseum* (as it is in the young bud of *E. apbyllum*) and the caudicles are apparently functionless. The detailed structure of *Stereosandra* is not well known, but the anther is erect and the pollinia bear caudicles. These genera probably are not very closely related to the Gastrodiinae, though, being saprophytes, they are superficially similar.

Epipogium, Stereosandra.

ORCHIDINAE (Angiadeniae Parlatores, Habenariinae Benthams, Serapiadiniae Benthams, Ophrydiniae Benthams & Hookers, Gymnadeniinae Pfitzers, Androcorydiniae Schltrs., Huttonaeinae Schltrs., Platantherinae Schltrs.)

The union of the Platantherinae and Habenariinae of Schlechter is certainly appropriate, when there is yet disagreement as to whether or not *Habenaria* and *Platanthera* are distinct genera. This group is seriously in need of monographic attention. The extreme "splitting" of European workers combined with the (equally unrealistic) extreme "lumping" of recent American workers has led to taxonomic chaos.

Aceratorchis, Aceras, Acrostylia, Amitostigma, Anacamptis, Androcorys, Arnottia, Bartolina, Benthamia, Bicornella, Bonatea, Brachycorythis, Centrostigma, Chamaeorchis, Coeloglossum, Cynorchis, Dactylorchis, Deroemera, Diphyllax, Diplacorchis, Diplomeris, Dithrix, Galeorchis, Gennaria, Gyaladenia, Gymnadenia, Habenaria, Herminium, Himantoglossum, Holotbrix, Huttonaea, Leucorchis, Loroglossum, Neobolusia, Neotinea, Neottiantbe, Nigritella, Obryas, Orchis, Peristylus, Perularia, Phyllomphax, Platanthera, Platycoryne, Roeperorchis, Schizochilus, Schwartzkopffia, Serapias, Stenoglottis, Steveniella, Traunsteinera, Tylostigma.

Tribe 5. EPIDENDREAE Lindley (Cereaceae Blume, Arethuseae Lindley, Gastrodieae Lindley, Malaxideae Lindley, Vandae Lindley, Kerosphaerae Schltr., all but 4 of Pfitzer's 31 tribes [1887], Sturmiae Pfitzer [1897]).

KEY TO SUBTRIBES

1. Growth sympodial, each shoot of limited growth and followed by other shoots from (usually basal) axillary buds (except *Vanilla* and *Galeola*, which are fleshy vines).....2
1. Growth monopodial, the inflorescence axillary and the stem usually growing indefinitely in length.....38
- 2 (1). Pollinia soft, mealy.....3
2. Pollinia in compact masses, more or less hard, waxy in texture.....7
- 3 (2). Sepals and petals more or less united (except in *Stigmatodactylus*); flowers often tubular; plants saprophytic (widespread).....GASTRODIINAE
3. Sepals and petals not united; plants autophytes or saprophytes.....4
- 4 (3). Plants with corms; stems short; leaves narrow and grass-like (North America and temperate Asia).....ARETHUSINAE
4. Plants without corms (except in *Nervilia*), stems elongate; leaves various.....5
- 5 (4). Leaves articulated at the base, deciduous (America and Africa).....SOBRALINAE
5. Leaves not articulated, persistent.....6

- 6(5). Seed with wing or sclerotic testa; fleshy vines, or sub-shrubs with a distinct calyculus below the ovary (widespread).....VANILLINAE
6. Seed without wing or sclerotic testa, seed coat thin and reticulate; plants not as above (widespread).....POGONIINAE
- 7(2). Inflorescence terminal or upper axillary, occasionally on young shoots before leaves develop (lateral and basal in a few species of *Epidendrum*, *Dendrobium*, *Coelogyne* and *Pleurothallis*).....8
7. Inflorescence lateral, usually basal.....25
- 8(7). Leaves plicate.....9
8. Leaves conduplicate.....16
- 9(8). Flowers borne on separate leafless shoots which alternate with the unifoliate vegetative shoots (Asia).....COLLABIINAE
9. Flowers and foliage borne on same shoot.....10
- 10(9). The pollinia naked, without caudicles (see also *Pseuderia*, *Dendrobiinae*) (widespread).
.....LIPARIDINAE
10. The pollinia bearing caudicles.....11
- 11(10). Pollinia 8.....12
11. Pollinia 2 or 4.....13
- 12(11). Flower with a distinct column foot and mentum (Asia, *Eria* alliance).....EPIDENDRINAE
12. Flower without a column foot or mentum (America and Africa).....SOBRALIINAE
- 13(11). Pseudobulbs or corms of a single internode; pollinia 4, usually without a viscidium (Asia).....COELOGYNINAE
13. Pseudobulbs or corms, if present, usually of several internodes.....14
- 14(13). Stems usually forming either corms or pseudobulbs; rostellum with a distinct viscidium (widespread).....CYRTOPODIINAE
14. Stems elongate, not forming corms or pseudobulbs; viscidium present or absent.....15
- 15(14). Plants Asiatic, usually with large, showy flowers.....THUNIINAE
15. Plants American, with small, inconspicuous flowers (*Palmorchis*).....SOBRALIINAE
- 16(8). Pollinia 2, 4, 6 or 8, clavate or laterally flattened.....17
16. Pollinia 2 and semi-globose or 4 and superposed.....22
- 17(16). Asiatic plants with elongate stems and terminal inflorescence of large showy flowers; pollinia 8.....THUNIINAE
17. Not with the above combination of features.....18
- 18(17). The ovary articulated to the pedicel, the pedicel persisting; pollinia clavate; plants without pseudobulbs (America).....PLEUROTHALLIDINAE
18. The ovary not articulated to the pedicel, the pedicel falling with the flower.....19
- 19(18). Pollinia naked, without caudicles (rarely with viscidium).....20
19. Pollinia with caudicles.....21
- 20(19). Flowers with a distinct column foot and mentum (except in *Pseuderia*) (widespread, predominantly Asiatic).....DENDROBIINAE
20. Flowers without a column foot or mentum (widespread).....LIPARIDINAE
- 21(19). Clinandrium more or less petaloid, overtopping the anther; pollinia 4; pseudobulbs of a single internode; inflorescence terminal (Asia).....COELOGYNINAE
21. Clinandrium usually not petaloid nor overtopping the anther; pollinia 2-8; pseudobulbs usually of several internodes; inflorescence often upper axillary (widespread).
.....EPIDENDRINAE
- 22(16). Plants with pseudobulbs.....23
22. Plants without pseudobulbs, stems elongate.....24
- 23(22). Pseudobulbs of a single internode; clinandrium petaloid and overtopping the anther; pollinia without a viscidium (Asia).....COELOGYNINAE
23. Pseudobulbs of several internodes; clinandrium not petaloid, nor overtopping anther, pollinia with a viscidium (*Polystachya*, largely African).....EPIDENDRINAE
- 24(22). Lip free from the column; flowers large (Asia).....THUNIINAE
24. Lip completely adnate to the column; flowers very small (*Epidanthus*, America).
.....EPIDENDRINAE
- 25(7). Leaves plicate.....26
25. Leaves conduplicate.....30

26(25).	Pseudobulbs or corms of several internodes, when present.....	27
26.	Pseudobulbs usually of a single internode (rarely absent in the <i>Zygopetalum</i> alliance).....	29
27(26).	Pollinia 4 or (usually) 8, clavate or laterally flattened, without stipe and usually without viscidium (widespread).....	BLETINAE
27.	Pollinia 2, or 4 and superposed, with a distinct viscidium and usually with a stipe.....	28
28(27).	Pollinia 2 or 4; plants usually with corms, sometimes with elongate pseudobulbs and basal inflorescence; lip often hinged or spurred (widespread).....	CYRTOPODIINAE
28.	Pollinia 4; plants with elongate pseudobulbs; inflorescences usually lateral on the pseudobulb; lip often saccate, but neither hinged nor spurred; anther usually sensitive, forcibly expelling the pollinia when triggered (America).....	CATASETINAE
29(26).	Lip immobile, often with antenna-like processes; flowers usually racemose (America).....	STANHOPEINAE
29.	Lip usually hinged at base and mobile, without antenna-like processes; flowers often solitary (America).....	MAXILLARIINAE
30(25).	Pollinia 2-8 (usually 4), clavate or laterally flattened, often without caudicle or stipe.....	31
30.	Pollinia 2, or 4 and superposed, usually with stipe and viscidium.....	36
31(30).	Pollinia naked, without caudicles, usually without a viscidium, never with stipe or caudicles.....	32
31.	Pollinia not naked, usually with distinct viscidium and stipe or caudicles.....	33
32(31).	Pollinia 2 or 4; inflorescence various (widespread, predominantly Old World).....	DENDROBIINAE
32.	Pollinia 8; inflorescence paniculate (New Guinea).....	RIDLEYELLINAE
33(31).	Flower with a pronounced column foot; stipe present, frequently double.....	34
33.	Column foot slight or absent; no true stipe present.....	35
34(33).	Lip and base of column more or less united into a tubular structure (Asia).....	THECOSTELINAE
34.	Lip free from column, not forming a tubular structure (Old World).....	GENYORCHIDINAE
35(33).	Pollinia 4, the caudicles inconspicuous; roots extremely thick (Ceylon and South India).....	ADROHIZINAE
35.	Pollinia 8, with a long caudicle; roots not especially thick (Asia).....	THELASINAE
36(30).	Pseudobulbs usually of several internodes (Old World).....	CYMBIDIINAE
36.	Pseudobulbs of a single internode.....	37
37(36).	Lip usually hinged to the base of the column, mobile; flowers usually solitary; often with a wide semilunate viscidium and short indistinct stipe (America).....	MAXILLARIINAE
37.	Lip not hinged to the base of the column, immobile; viscidium usually compact, clearly differentiated from the stipe (America).....	ONCIDIINAE
38(1).	Clinandrium petaloid, overtopping anther; small American plants.....	PACHYPHYLLINAE
38.	Clinandrium not petaloid, not overtopping the anther.....	39
39(38).	Old World plants.....	40
39.	American plants.....	41
40(39).	Pollinia 8, without a stipe (but with a long caudicle).....	THELASINAE
40.	Pollinia 2 or 4, with a distinct stipe (see also <i>Dipodium</i> , <i>Cymbidiinae</i>).....	SARCANTHINAE
41(39).	Flower with a distinct spur.....	42
41.	Flowers without spurs (except in <i>Rodriguezia</i> , <i>Oncidiinae</i>).....	43
42(41).	Flowers in racemes, or plants leafless; spur not concealed by a bract.....	SARCANTHINAE
42.	Flowers solitary; spur parallel with the pedicel and usually concealed by a bract; plants leafy.....	CRYPTOCENTRINAE
43(41).	Lip hinged to the base of the column, mobile; flowers usually solitary, often with a wide semilunate viscidium and a short indistinct stipe.....	MAXILLARIINAE
43.	Lip not hinged to the base of the column, immobile; viscidium usually compact, clearly differentiated from the stipe.....	ONCIDIINAE

ADRORHIZINAE Schltr.

Schlechter placed this group near the Coelogyninae, while Kränzlin allied them to *Dendrobium* or *Eria*. These views are not necessarily opposed, as we believe the Coelogyninae and Epidendrinae (esp. *Eria*) to be closely related. These genera appear to be closest to *Eria*, but are distinguished by the lateral inflorescence and fewer pollinia.

Adrorhizon, *Josephia*.

ARETHUSINAE Benth (Bletillinae Schltr.)

These largely north temperate genera have corms or fleshy rhizomes and closely resemble the Bletiinae, but the pollinia are mealy and without caudicles. *Crybe* and *Jimensia* may well be more closely related to *Bletia* than to *Arethusa*.

Arethusa, *Calopogon*, *Crybe*, *Jimensia* (*Bletilla*).

BLETIINAE Benth (Chysiinae Schltr., Phajinae Schltr.)

Chysis is apparently allied to *Acanthephippium*. *Coelia* and *Bothriochilus* are placed here on the subuplicate leaves, the lateral inflorescence and the relatively soft, subclavate pollinia. They do not show close relationship to the genera of the Epidendrinae. *Basiphyllaea*, similarly, is out of place among the Epidendrinae; it seems to differ from *Bletia* primarily in size. *Hexalectris* is closely allied to *Bletia*, and less so to *Chysis*. *Bletia* closely resembles some species of *Laelia* (Epidendrinae) in flower structure, and these genera may be more closely related than is indicated by our present classification.

Acanthephippium, *Ancistrochilus*, *Anthogonium*, *Ascotaenia*, *Aulostylis*, *Basiphyllaea*, *Bletia*, *Bothriochilus*, *Calanthe*, *Chysis*, *Coelia*, *Gastorchis*, *Hexalectris*, *Ipsa*, *Pachystoma*, *Phajus*, *Plocoglottis*, *Spathoglottis*, *Taeniopsis*.

CATASETINAE Schltr.

This is an interesting group because of the usually sensitive anther, but some species of *Catasetum* (or *Clowesia*) lack this feature. These genera are apparently related to the Cyrtopodiinae (especially *Cyrtopodium* and *Galeandra*).

Catasetum, *Cynoches*, *Mormodes*.

COELOGYNINAE Benth

The flower structure of this group is close to that of the Epidendrinae and Bletiinae, but the habit is distinctive, and the pollinia are superposed in some genera.

Acoridium, *Basigyne*, *Bulleyia*, *Coelogyne*, *Dendrobilum*, *Dicksonia*, *Gynoglottis*, *Ischnogyne*, *Nabalua*, *Neogyne*, *Otocbilus*, *Panisea*, *Pholidota*, *Pleione*, *Pseudacoridium*, *Sigmatogyne*.

COLLABIINAE Schltr.

These genera seem to be very closely allied to both the Bletiinae and the Cyrtopodiinae. *Taivia* and *Nephelephyllum* are certainly allied to *Eulophia*. The

habit of this group is relatively distinctive, while the structure of the pollinia is somewhat diverse.

Chrysoglossum, *Collabium*, *Diglyphosa*, *Hancockia*, *Mischobulbon*, *Nephelaphyllum*, *Pilophyllum*, *Tainia*.

CRYPTOCENTRINAE Garay

These genera were placed in the Maxillariinae by Schlechter, apparently because of the habit and 1-flowered inflorescence. Schlechter considered *Sepalosaccus* (which we have not seen) to be intermediate between *Maxillaria* and *Cryptocentrum*. Garay has created a separate subtribe for *Cryptocentrum*, on the basis of the conspicuous spur (other features listed by Garay are present in the *Maxillaria* alliance or are different aspects of the spur). According to Garay, *Cryptocentrum* would find its closest affinity in the Oncidiinae, but we are unable to agree with this conclusion. We believe that the genus most closely approaches *Trigonidium* (Maxillariinae). *Cryptocentrum* is usually monopodial, but sympodial species occur. The genus is rather distinctive and may merit a separate subtribe, but further study is needed.

Anthosiphon, *Cryptocentrum*.

CYMBIDIINAE Benthams

The Cymbidiinae bear a general resemblance to the Bletiinae, but seem to be distinct in both habit and structure of pollinia. A single hybrid between *Phajus* and *Cymbidium* is recorded. Rolfe (1911) has shown that this parentage is probably in error. Many more recent attempts to cross these genera have failed. *Ansellia* closely resembles *Grammatophyllum* and, like that genus, has conduplicate leaves and sometimes bears lateral inflorescences (while *Grammatophyllum* may rarely produce a terminal inflorescence). *Ansellia* must be placed in the Cymbidiinae, if this group can be maintained separate from the Cyrtopodiinae. Perrier (1941) assigns *Grammangis* and *Cymbidiella* to the Cyrtopodiinae and suggests that the two groups cannot be separated. The Cymbidiinae generally have elongate stems or pseudobulbs with several or many leaves, while the few Cyrtopodiinae which have conduplicate leaves usually have very short, unifoliate pseudobulbs, but this is surely not a very convincing separation; further study is needed. Holttum (1958) indicates the probable relationships of this subtribe to the Sarcanthinae, from which a few monopodial species are not easily distinguished by any "key" feature. *Acriopsis* resembles *Porphyroglottis*, but is unusual in the petaloid clinandrium, the union of the lip and column, and the form of the pollinia. It may deserve a separate subtribe, but it is not closely allied to *Thecostele*.

Acriopsis?, *Ansellia*, *Caloglossum*, *Cymbidiella*, *Cymbidium*, *Cyperorchis*, *Dipodium*, *Grammangis*, *Grammatophyllum*, *Poicilanthus*, *Porphyroglottis*.

CYRTOPODIINAE Benthams (Eulophiinae Benthams, Corallorhizinae Schltr., Calypsoinae Schltr., Eulophidiinae Schltr.)

Several of these genera were placed in the Polystachyinae by Schlechter, but they show little affinity to *Polystachya*, and are separated from the Cyrtopodiinae only by the position of the inflorescence. The peculiar anther of *Galeandra* is duplicated

in some species of *Eulophia* (and among the Collabiinae). *Corallorbiza* is clearly allied to *Oreorchis* and *Aplectrum*. While brought together from diverse parts of Schlechter's system, this forms one of the more natural subtribes. It is usually characterized by corms (rhizomes in the saprophytes, pseudobulbs in some species of *Galeandra*, *Eulophia* and *Cyrtopodium*), plicate leaves and 2 or 4 (superposed) pollinia with a distinct viscid disk, but little or no stipe. The lip and column of *Calypso* are distinctive, but it is apparently related to *Dactylostalix* and *Yoania*, which are more characteristic of the subtribe. For the placement of *Yoania* in this group, see Finet (1896). *Cyrtopodium* is somewhat distinctive in habit and the form of the lip, but the habit is approached by some species of *Eulophia* and *Galeandra*. Schlechter's inclusion of *Eulophia* in the Cyrtopodiinae would seem to require the use of this name, rather than Eulophiinae, for this group.

Schlechter assigns *Eulophidium* to a separate subtribe, but Mansfeld places it in the Cyrtopodiinae. Perrier (1941) goes so far as to treat *Eulophidium* as a subgenus of *Lissochilus*. The American species are distinctive in habit and closely resemble *Oncidium* section *Miltoniastrum*. This section of *Oncidium* has relatively simple rostellar structure, and it is possible that *Eulophidium* represents a phyletic link between the Cyrtopodiinae and the Oncidiinae.

Acrolophia, *Calypso*, *Corallorbiza*, *Cremastra*, *Cyanaeorchis*, *Cyrtopodium*, *Dactylostalix*, *Eulophia*, *Eulophidium*, *Eulophiella*, *Galeandra*, *Geodorum*, *Govenia*, *Graphorkis*, *Lissochilus*, *Pteroglossaspis*, *Tipularia*, *Warrea*, *Yoania*.

DENDROBIINAE Benth (Bulbophyllinae Schltr.)

We follow Benth in associating *Dendrobium* and *Bulbophyllum* in a separate subtribe. We do not doubt that *Dendrobium* is related to *Eria*, but the relationship to *Bulbophyllum* is much closer, and the naked pollinia of this group are quite distinctive. *Dendrobium* and *Bulbophyllum* are primarily distinguished by the position of the inflorescence, and even this is subject to exceptions, as in *D. laterale* L. Wms. The embryological data also support a close relationship between these genera (Swamy, 1949). These are probably the largest genera of the orchids, as now treated. Holttum (1953) notes that the sections of *Dendrobium* are biologically far more distinct than many orchid genera in other subtribes. It may be that the naked pollinia severely limit the possibilities of morphological variation in flower structure. Generic limits in the Liparidinae (with naked pollinia) are similarly difficult. If this hypothesis is correct, the Genyorchidinae, which are surely derived from *Bulbophyllum*-like ancestors, may have escaped these limitations by the development of stipes, and show correspondingly greater variation in flower structure.

Bulbophyllum, *Dendrobium*, *Epigeneium*, *Pedilochilus*, *Pseuderia*, *Saccoglossum*.

EPIDENDRINAE (Eriinae Benth, Laeliinae Benth, Stenoglossinae Benth, Podochilinae Benth & Hooker, Cattleyinae Pfitzer, Ponerinae Pfitzer, Glomerinae Schltr., Polystachyinae Schltr., Epidanthinae L. Wms.)

We are relatively familiar with the genera of this group, especially the American ones, and we have found it necessary to unite several previously recognized

subtribes under this one. It is quite possible that some of the alliances which are discussed below will eventually prove to deserve subtribal status, but we are unable to find any feature or combination of features which will convincingly separate them. The key features which have been used are largely imaginary. The name *Epidendrinae* is required for the subtribe of the *Epidendreae* which includes the type genus. Hawkes and Heller (1959) list the "subtribe *Stolzinae*," but we have not been able to locate any valid publication of such a name. Schlechter (1926) and Summerhayes (1953) agree that *Stolzia* is closely related to *Polystachya*.

KEY TO ALLIANCES

1. Pollinia laterally flattened or subglobose, 2-8.....2
1. Pollinia clavate, 4-8.....4
- 2(1). Plants African (except for some species of *Polystachya*—pseudobulbous plants with terminal raceme, a distinct column foot, 2-4 pollinia, a distinct viscidium, and the callus of the lip usually with mealy hairs).....*Polystachya* alliance
2. Plants not African.....3
- 3(2). Plants American; pollinia 2-8; inflorescence usually terminal.....*Epidendrum* alliance
3. Plants Asiatic; pollinia 8; inflorescence usually upper axillary.....*Eria* alliance
- 4(1). Rostellum elongate, beak-like; anther dorsal.....7
4. Rostellum short, not markedly projecting nor beak-like; anther more or less terminal.....5
- 5(4). Plants American, with slender, unifoliate stems, fleshy leaves and a dense spike of small rose-purple flowers.....*Arpophyllum* alliance
5. Plants of Old World.....6
- 6(5). Viscidium well developed; flowers usually in dense subcapitate clusters.....*Glomera* alliance
6. Viscidium usually absent; flowers not in dense subcapitate clusters.....*Eria* alliance
- 7(4). Asiatic plants with elongate stems and distichous leaves.....*Podochilus* alliance
7. American plants with short, unifoliate stems (*Meiracyllium*).....*Arpophyllum* alliance

a. ARPOPHYLLUM ALLIANCE

These two genera stand apart from the *Epidendrum* alliance in the possession of clavate rather than laterally flattened pollinia. The form of the pollinia and viscidium ally them to the *Glomera* and *Podochilus* alliances, and, especially, to the *Pleurothallidinae*, with which they agree in habit. They probably represent the ancestral stock of this distinctive American subtribe.

Arpophyllum, *Meiracyllium*.

b. EPIDENDRUM ALLIANCE

The classic distinction between the *Laeliinae* and the *Ponerinae*; the presence or absence of a column foot, is clearly an unnatural one, and largely a matter of degree. The column foot is slight in several of the genera, and, in fact, is present in some species of *Laelia* (in the section *Schomburgkia*). Several genera have been repeatedly shifted between the two groups, as for example *Domingoa*, *Nageliella* and *Hexisea*. *Domingoa*, though closely related to *Nageliella* and *Scaphyglottis*, has been crossed with *Encyclia*. *Nageliella* is clearly allied to some of the elements of the *Scaphyglottis* complex; and *Homalopetalum*, *Hexisea* and *Nidema*, similarly, show greater affinity to *Scaphyglottis* than to the other plants customarily included in the *Laeliinae*.

Williams has separated *Epidanthus* as a subtribe, on the basis of a distinct

viscidium. Such a viscidium, however, is found in most species of *Epidendrum*. *Epidanthus* is distinctive in the possession of only two pollinia, but in all other features it resembles true *Epidendrum*.

This alliance appears to be the most distinctive of those included here, and it is possible that it is not as closely related to *Eria* as the structure of *Ponera*, especially, suggests. It may be that the resemblances between *Ponera* and *Eria* are parallelisms, and not indicative of close relationship. We are reluctant, though, to recognize subtribes on the basis of distribution alone.

Alamania, *Barkeria*, *Brassavola*, *Broughtonia*, *Cattleya*, *Caularthron*, *Constantia*, *Dimerandra*, *Diothonea*, *Domingoa*, *Encyclia*, *Epidanthus*, *Epidendrum*, *Hexisea*, *Homalopetalum*, *Isabelia*, *Isochilus*, *Jacquinella*, *Laelia*, *Leptotes*, *Loefgrenianthus*, *Nageliella*, *Neocogniauxia*, *Nidema*, *Octadesmia*, *Orleanesia*, *Platyglottis*, *Ponera*, *Scaphyglottis*, *Sophranitella*, *Sophranitis*, *Tetramicra*.

c. ERIA ALLIANCE

This group is not clearly separable from either the *Epidendrum* alliance or the *Polystachya* alliance. The three may be thought of as the American, Asiatic and African segments of a single complex, though a few species of *Polystachya* are widespread.

Cryptochilus, *Eria*, *Porpax*.

d. GLOMERA ALLIANCE

These genera are very closely allied to *Eria*, though the viscidium is better developed. The two groups may not merit separation, even as alliances.

Aglossorhyncha, *Agrostophyllum*, *Ceratostylis*, *Chitonochilus*, *Cyphochilus*, *Earina*, *Epiblastus*, *Giulianettia*, *Glomera*, *Glossorhyncha*, *Ischnocentrum*, *Mediocalcar*, *Poaephyllum*, *Sarcostoma*, *Sepalosiphon*.

e. PODOCHILUS ALLIANCE

This group is closely allied to the *Glomera* alliance, and differentiated primarily by the more elongate rostellum.

Appendicula, *Chilopogon*, *Podochilus*.

f. POLYSTACHYA ALLIANCE

These genera show little affinity to the other genera grouped in the *Polystachyinae* by Schlechter. *Neobenthamia* has four laterally flattened pollinia and an indistinct viscidium (many species in the *Epidendrum* alliance have the viscidium better developed), while *Stolzia* has eight pollinia and no viscidium. *Polystachya* has a distinct viscidium and the pollinia are united into two in some species, while others bear four laterally flattened pollinia, as in the majority of the *Epidendrinae*. Some species of *Polystachya* have a small but distinct stipe, while this is not evident in other species which we have examined.

Neobenthamia, *Polystachya*, *Stolzia*.

GASTRODIINAE Pfitzer

The *Gastrodiinae* are all saprophytic, and the flowers are tubular in most species.

They are apparently allied to the Vanillinae and Pogoniinae. *Stigmatodactylus* is clearly out of place in the Chloracinae (Acianthinae), and appears to be closely allied to *Didymoplexis* section *Leucolaena* (*Didymoplexiella*).

Auxopus, *Didymoplexis*, *Gastrodia*, *Stigmatodactylus*?, *Uleiorchis*.

GENYORCHIDINAE Schltr.

This group is allied to the Dendrobiinae, and especially to *Bulbophyllum*, but apparently differs in the possession of a distinct stipe or stipes.

Drymoda, *Genyorchis*, *Ione*, *Monomeria*.

LIPARIDINAE Benth (Microstylidinae Benth, Malaxidinae Benth & Hooker, Vargasiellinae C. Schweinf. [not validly published])

This subtribe, like the Dendrobiinae, is distinctive in the possession of completely naked pollinia. A viscidium is sometimes developed, but caudicles are lacking. The systematic position of the Liparidinae is not well understood. Mansfeld suggests a relationship to the Cyrtopodiinae (Calypsoinae), as well as to the Neottinae (tribe Neottieae), but neither relationship is well documented. Clearly, this group deserves further study.

The subtribe Vargasiellinae was proposed without description, and is thus not validly published. The only clear feature we can find which might be taken to distinguish *Vargasiella* from the Liparidinae is the distinct claw of the lip. The habit is distinctive among the American genera, but is less so when Old World genera are considered. This genus should also be compared with *Pseuderia* (Dendrobiinae).

Didickea?, *Ephippianthus*?, *Hippeophyllum*, *Imerinaea*, *Liparis*, *Malaxis*, *Oberonia*, *Orestia*, *Risleya*, *Vargasiella*.

MAXILLARIINAE Benth (Huntleyinae Schltr., Lycastinae Schltr., Zygopetalinae Schltr.)

We are unable to separate the Huntleyinae and Zygopetalinae even as alliances (see below). The close relationship between the *Lycaste* and *Zygopetalum* alliances is confirmed by artificial hybrids such as *Zygocaste*. The *Maxillaria* alliance is superficially separated from the *Lycaste* alliance by the conduplicate leaves, but floral structure indicates a close relationship. The structure of the pollinia is similar in *Xylobium*, *Bifrenaria* and *Maxillaria*. Of interest is *Bifrenaria minuta* Garay, which has slightly plicate leaves, but is otherwise a *Maxillaria*. We know of a hybrid between *Lycaste virginalis* and *Maxillaria variabilis*, though none of the plants has yet flowered. The difficulty of raising *Lycaste* seedlings to maturity is probably one reason that no such hybrids are yet registered.

KEY TO ALLIANCES

- | | | |
|-------|--|-----------------------------|
| 1. | Callus usually wide, with conspicuous longitudinal ridges..... | <i>Zygopetalum</i> alliance |
| 2. | Callus usually narrow, smooth..... | 2 |
| 2(1). | Leaves plicate..... | <i>Lycaste</i> alliance |
| 2. | Leaves conduplicate..... | <i>Maxillaria</i> alliance |

a. LYCASTE ALLIANCE

We have placed *Teuscheria* here, though its author assigned it to the *Bletiinae*. The shape of the anther and the four superposed pollinia with a distinct viscidium (large in *T. pickiana*, quite small in *T. venezuelana*) support this classification. The genus is described as lacking a viscidium, but we do not understand "Pollinia . . . inappendiculata, visco parco cohaerentia, sine glandula." The viscidium (and the resupinate flower) is clearly shown in Mrs. Allen's illustration of *T. pickiana* (Ceiba 4:272. 1955). *Neomoorea* and *Eriopsis* are assigned to the *Zygopetalinae* by Mansfeld (1937), but appear to fit as well or better in the *Lycaste* alliance.

Anguloa, *Bifrenaria*, *Eriopsis*?, *Lycaste*, *Neomoorea*?, *Rudolfiella*, *Teuscheria*, *Xylobium*.

b. MAXILLARIA ALLIANCE

Hoehne has separated some of the monopodial *Maxillarias* as a distinct genus, *Marsupiaria*, but it is doubtful that this is a natural group. *Maxillaria valenzuelana*, for example, is extremely closely related to *M. crassifolia* (a sympodial species) in all floral features, and seedlings of *M. crassifolia* have the habit of *M. valenzuelana*.

Chrysocycnis, *Cyrtidium*, *Maxillaria*, *Mormolyca*, *Pityphyllum*, *Scuticaria*, *Sepalosaccus*, *Trigonidium*.

c. ZYGOPETALUM ALLIANCE

The *Huntleyinae* are traditionally separated from the *Zygopetalinae* by the conduplicate leaves, but this distinction is not usable. The leaves are subplicate in most species. We have observed cases in both *Zygopetalum mackayi* and *Cochleanthes flabelliformis* in which young growths with conduplicate veneration were seen in the same plant with growths of distinctly convolute veneration. The genera assigned to the *Zygopetalinae* usually have pseudobulbs, while those assigned to the *Huntleyinae* usually have the pseudobulbs inconspicuous or none. Some genera of this alliance, such as *Otostylis*, strongly resemble the *Cyrtopodiinae*, and suggest the origin of this subtribe from *Eulophia*-like ancestors.

Aganisia, *Batemannia*, *Bollea*, *Cheiradenia*, *Chondrorhyncha*, *Cochleanthes*, *Colax*, *Galeottia*, *Huntleya*, *Koellensteinia*, *Menadenium*, *Neogardneria*, *Otostylis*, *Paradisiantbus*, *Pescatoria*, *Promenaea*, *Stenia*, *Warella*, *Zygopetalum*.

ONCIDIINAE Benth (Notyliinae Benth, Adinae Pfitzer, Aspsiinae Pfitzer, Ionopsidinae Pfitzer, Odontoglossinae Pfitzer, Trichopiliinae Pfitzer, Bractiinae Schltr., Campanemiinae Schltr., Cochliodinae Schltr., Compartmentiinae Schltr., Dichaeinae Schltr., Lockhartiinae Schltr., Macradeniinae [Mansf.] Schltr., Ornithocephalinae Schltr., Papperitzinae Schltr., Pterostemminae Schltr., Saundersiinae Schltr., Telipogoninae Schltr., Trichocentrinae Schltr.)

It is in this group that we have committed the most wholesale reduction of subtribes. These changes, however, are required not only by the rapidly accumulating evidence of intergeneric fertility (see Moir, 1959), but by the patterns of morphological variation as well. Some of the "genera" placed in separate subtribes by Schlechter can not be distinguished by any feature known to us.

KEY TO ALLIANCES

1. Pollinia 2.....*Oncidium* alliance
1. Pollinia 4.....2
- 2(1). Column with elongate, beak-like rostellum; lip not anchor-shaped...*Ornithocephalus* alliance
2. Column with a short rostellum, not beak-like; lip usually anchor-shaped.....*Dichaea* alliance

a. DICHAEA ALLIANCE

This genus is distinctive in habit and aspect, but closely related to the *Ornithocephalus* alliance. The pilose column with a "ligule" on the ventral surface is also found in *Telipogon* and allied genera.

Dichaea.

b. ONCIDIUM ALLIANCE

It might seem, from a survey of Schlechter's classification, that there would be a valid break within this group into two major alliances, those with spurs and those without. The presence or absence of a spur, however, is not consistent within the genera, and these groups are nearly all interfertile. We have successfully crossed *Compartmentia* with *Oncidium*, *Trichocentrum*, *Trichopilia* and *Ionopsis*. *Rodriguezia*, similarly, is interfertile with a wide range of genera. *Trichopilia* is superficially distinct, in that the base of the lip enfolds the column, but this same feature is found in some species of *Miltonia*. *Notylia* is unusual in the dorsal position of the anther, but this, too, is inconsistent. *Lockhartia* is distinctive in habit, but has no other consistent feature to distinguish it from the other genera of this group. *Pterostemma* is poorly known, but its monopodial habit can not be taken to exclude it from this subtribe.

Ada, *Amparosa*, *Aspasia*, *Brachtia*, *Brassia*, *Capanemia*, *Caucaea*, *Chaenanthus*, *Cochlidia*, *Cobniella*, *Compartmentia*, *Diadenium*, *Erycina*, *Gomesa*, *Hybochilus*, *Ionopsis*, *Leocbilus*, *Lockhartia*, *Macradenia*, *Mesospinidium*, *Miltonia*, *Neodryas*, *Neokoeberia*, *Notylia*, *Odontoglossum*, *Oncidium*, *Pappperitzia*, *Petalocentrum*, *Polyotidium*, *Plectrophora*, *Pterostemma*, *Quekettia*, *Rodriguezia*, *Rodriguezioopsis*, *Roezliella*, *Rusbyella*, *Sanderella*, *Saundersia*, *Scelochilus*, *Sigmatostalix*, *Solenidium*, *Systeloglossum*, *Sutrina*, *Theodorea*, *Trichocentrum*, *Trichopilia*, *Trizeuxis*, *Warmingia*.

c. ORNITHOCEPHALUS ALLIANCE

These genera are distinguished from the *Oncidium* alliance only by the number of pollinia, but they do form a somewhat distinctive group. There is no way, however, to separate the *Telipogoninae* and the *Ornithocephalinae*. Many of the *Telipogoninae* are distinctive in that they apparently mimic insects (as in many species of *Ophrys*), and in the pilose column and hooked viscidium, but these latter features are matched by *Cordanthera* and some species of *Dipteranthus*.

Centroglossa, *Chytroglossa*, *Cordanthera*, *Cryptarrhena*, *Dipteranthus*, *Dipterostele*, *Hintonella*, *Hofmeisterella*, *Oakes-amesia*, *Ornithocephalus*, *Phymatidium*, *Platyrhiza*, *Sodiocella*, *Sphyrastylis*, *Stellilabium*, *Telipogon*, *Thysanoglossa*, *Trichoceros*, *Zygostates*.

PACHYPHYLLINAE Pfitzer

Though distinguished by the differently shaped column and consistently monopodial habit, these genera seem closely allied to the *Maxillariinae*. *Pachyphyllum*

and *Chrysocycnis*, especially, appear to be closely allied, and resemble each other in habit, inflorescence and 3-winged ovary.

Centropetalum, *Pachyphyllum*.

PLEUROTHALLIDINAE Benth

These genera form a distinctive American group most closely allied to the Epidendrinae, especially to the *Arpophyllum* alliance.

Acostaea, *Barbosella*, *Brachionidium*, *Cryptophoranthus*, *Lepanthes*, *Lepanthopsis*, *Masdevallia*, *Octomeria*, *Physosiphon*, *Platystele*, *Pleurothallis*, *Pleurothallopsis*, *Porroglossum*, *Restrepia*, *Scaphosepalum*, *Stelis*, *Yolanda*.

POGONIINAE Pfitzer (Nerviliinae Schltr.)

We follow Mansfeld in separating the Vanillinae and the Pogoniinae, and including *Nervilia* in the Pogoniinae. The flower structure of *Nervilia* is quite comparable to that of the other Pogoniinae, and most species were first described under *Pogonia*. The habit is somewhat distinctive. These genera are similar in floral structure to both the Vanillinae and the Sobraliinae. The pollen is quite mealy, but they lack the distinctive seed structure of the Vanillinae.

Cleistes, *Isotria*, *Lecanorchis*, *Monophyllorchis*, *Nervilia*, *Pogonia*, *Pogoniopsis*, *Psilochilus*, *Triphora*.

RIDLEYELLINAE Schltr.

The habit of this genus is suggestive of *Bulbophyllum*, and the pollinia are said to be naked, though the floral structure is otherwise more reminiscent of the Thelasiinae.

Ridleyella.

SARCANTHINAE Benth (Aeridinae Pfitzer)

This is the great group of primarily Old World monopodial orchids. In floral specialization and complexity they parallel the American Oncidiinae and are not easily "keyed" from the monopodial Oncidiinae, though there is probably no close relationship. Note that this group must be known as the Vandinae if the tribe Vandae is maintained. Hawkes and Heller (1959) list the "subtribe Campylocentrinae." This name is listed by Hoehne in *Flora Brasílica* (12¹:23, 39), but we cannot find that it has ever been formally proposed, nor can we find any reason that it should be.

Abdominea, *Acampe*, *Adenoncos*, *Aerangis*, *Aeranthus*, *Aerides*, *Ambrella*, *Ancistrorhynchus*, *Angraecopsis*, *Angraecum*, *Ankylocheilus*, *Arachnis*, *Armadorum*, *Ascocentrum*, *Ascochilopsis*, *Ascoglossum*, *Barombia*, *Bathiea*, *Beclardia*, *Bogoria*, *Bolusiella*, *Bonniera*, *Calymmanthera*, *Calyptrochilus*, *Camarotis*, *Campylocentrum*, *Ceratocbilus*, *Chamaeangis*, *Chamaeantbus*, *Chauliodon*, *Cheirorchis*, *Cbiloschista*, *Chroniobchilus*, *Cottonia*, *Crossangis*, *Cryptopus*, *Cyrtorchis*, *Dendrophylax*, *Diaphnanthe*, *Dinklageella*, *Diplocentrum*, *Diploprosa*, *Dryadorchis*, *Eggelingia*, *Encheiridion*, *Esmeralda*, *Eurychone*, *Finetia*, *Fitzgeraldiella*, *Gastrochilus*, *Holcoglossum*, *Hymenorchis*, *Jumellea*, *Lemurella*, *Lemurorchis*, *Listrostachys*, *Luisia*, *Macropodanthus*, *Malleola*, *Microcoelia*, *Microsaccus*, *Microtatorchis*, *Mystacidium*, *Nephrangis*, *Neobathiea*, *Oeonia*, *Oeoniella*, *Omoea*, *Ornithobchilus*, *Pelatantheria*, *Pennilabium*, *Perrierella*, *Phalaenopsis*, *Phormangis*, *Phragmorchis*, *Plectrelminthes*, *Podangis*, *Polyrbiza*, *Pomatocalpa*, *Porphyrodesme*, *Rangaeris*, *Renanthera*,

Renantherella, *Rhipidoglossum*, *Rhynchosstylis*, *Robiquetia*, *Saccolabiopsis*, *Saccolabium*, *Sarcantbus*, *Sarcocbilus*, *Sarcorrhynchus*, *Schoenorchis*, *Solenangis*, *Sphyrarhynchus*, *Staurochilus*, *Stauropsis*, *Taeniophyllum*, *Taeniorrhiza*, *Thrixspermum*, *Triceratorhynchus*, *Trichoglottis*, *Tridactyle*, *Uncifera*, *Vanda*, *Vandopsis*, *Ypsilopus*.

SOBRALIINAE Schltr. (Palmorchidinae Schweinf. & Correll [not validly published])

These genera were included in the Neottieae by Schlechter, but the pollinia are more or less waxy in many species, and the flower structure agrees well with that of the Epidendrinae and Thuniinae. Mansfeld actually assigns the Thuniinae to this subtribe, though we believe this action to be questionable, at least without more detailed knowledge of the Thuniinae. Schweinfurth has evidently abandoned the use of the subtribe Palmorchidinae, which was proposed without description. In no case did Schweinfurth and Correll assign *Corymborchis* to the Palmorchidinae, an action which would scarcely have been defensible (see, however, Hawkes & Heller, 1959).

Diceratostele, *Elleanthus*, *Palmorchis*, *Sertifera*, *Sobralia*, *Xerorchis*.

STANHOPEINAE Benth (Gongorinae Schltr.)

This group is not clearly distinguished from the Maxillariinae (*Lycaste alli-ance*), though the more bizarre genera (*Stanhopea*, *Coryanthes*, etc.) are easily distinguished. More study of this group is needed.

Acineta, *Chaubardia*?, *Cirrhaea*, *Coeliopsis*, *Coryanthes*, *Endresiella*, *Gongora*, *Gorgoglossum*, *Houlletia*, *Kegeliella*, *Lacaena*, *Lueddemannia*, *Lycomormium*, *Papbinia*, *Peristeria*, *Polycycnis*, *Schlimia*, *Sievekingia*, *Stanhopea*, *Trevoria*.

THECOSTELINAE Schltr.

The flower structure of *Thecostele* is quite bizarre, but adequate knowledge of all species may indicate that it should be included in the Genyorchidinae.

Thecostele.

THELASIINAE Schltr.

The Thelasiinae are small Asiatic plants which are distinctive in habit and inflorescence. The pollinia have been described as having a stipe, but this appears to be an unusually long caudicle (Mansfeld, 1937b).

Chitonanthera, *Octarrhena*, *Oxyanthera*, *Phreatia*, *Rhynchophreatia*, *Thelasis*.

THUNIINAE Schltr. (Claderiinae Mansf. [not validly published])

Tall Asiatic plants with slender stems and rather showy flowers, in habit these plants (especially *Arundina*) closely resemble the Epidendrinae. In the structure of the column, however, they more closely resemble *Coelogyne* and *Phajus*. *Bromheadia* was placed in the Polystachyinae by Schlechter, but is surely out of place there (see Ridley, 1891). It resembles *Dilochia* in habit and appears to resemble *Claderia* in flower structure. Unfortunately, we have seen too little of all these genera. The group is unusually diverse in the structure of the pollinia, and it is possible that further study will show it to be unnatural. The subtribe Claderiinae was proposed without description.

Arundina, *Bromheadia*?, *Claderia*, *Dilochia*, *Thunia*.

VANILLINAE Bentham

These genera are, in several features, among the most primitive in the subfamily. They are included in the Pogoniinae by Schlechter, but the habit and distinctive seed structure would seem to justify their separation, as indicated by Mansfeld. They also show some affinity to the Sobraliinae, but there is little evidence of close alliance with the Neottieae.

Duckeella, Epistephium, Eriaxis, Galeola, Vanilla.

SUBTRIBES OF UNCERTAIN AFFINITY

GROBYINAE Schltr.

This genus has been placed near the Cymbidiinae in most systems, but this seems to be questionable. We have not seen adequate material, but a comparison with the Maxillariinae may be in order.

Grobya.

PACHYPLECTRINAE Schltr.

This genus is known only from New Caledonia. It apparently belongs to the Neottieae, but Schlechter's description is not adequate for more exact placement. It may be allied to the Diuridinae and Cryptostylidinae.

Pachyplectron.

PHYLOGENY

There are two extremes in the variation patterns shown by living plant groups, depending apparently on rates of evolution and amount of extinction. At one end of the spectrum stand such families as the Magnoliaceae, Annonaceae and Nymphaeaceae. These families have the appearance of being "old" groups, in which evolution is proceeding at a leisurely pace and extinction has greatly affected the pattern of variation. Such groups as the cacti and the Euphorbiaceae-Euphorbieae represent the other extreme. They show little evidence of great age, show signs of relatively rapid diversification in geologically recent time, and give much less evidence of extinction. Our classification of genera and higher groups is in large measure based on extinction, and so we have very different problems with these two types. The delimitation of genera and tribes within the Magnoliaceae or the Nymphaeaceae is not difficult. We are often at a loss, though, to understand their relationships or phylogeny.

As should now be clear, the orchids are near the other end of our spectrum in these features. Genera are often difficult to define, and higher categories within the family seem even worse. These hazy boundaries between tribes and subtribes, however, may give clues to the patterns of phylogeny within the family. We do not mean to imply that living groups can often be derived from other living groups, but one can find excellent evolutionary series for nearly every morphological feature within the orchids. In recent years there has been a healthy skepticism concerning phylogenetic schemes (see especially Sporne, 1959). Even

when one can find a good morphological series in some feature, it is often difficult to decide in which direction or directions evolution has occurred. This problem is not so serious in a highly derived group such as the Orchidaceae. In comparing *Cephalanthera* and *Oncidium* there can be little doubt as to which is derived and which is primitive. In nearly every feature in which these two differ, it is *Cephalanthera* which is the ordinary monocot, easily comparable with other monocot families, while *Oncidium* can scarcely be understood without comparing it with the less specialized members of the family. One would scarcely expect to derive whorls of separate stamens and pistils from the column of the advanced Epidendreae, but the evolution of the column from primitively free parts is easily understood and partially documented among the living orchids. As an actively evolving group in which the patterns of evolution are unusually clear, the orchids are especially appropriate for evolutionary study and may throw a good deal of light on parallelism, polyphyletic and other problems which plague the biologist dealing with apparently more ancient groups.

When one studies the relationships of the subtribes, a pattern takes shape, and one may form a rather clear idea of the over-all evolutionary patterns for the family. The pattern of relationships for the Epidendreae (fig. 1) scarcely provides a classic dendrogram, but there are clear indications of primitive groups and some indications of the patterns of evolution which may have occurred. These may best be considered by discussing evolution in particular features of the plant.

HABIT

As Holttum (1955) has shown, the predominant growth form in a wide range of monocots is the sympodium, and we may reasonably consider this to be the primitive condition in the orchids. The majority of primitive orchids have a rather ordinary monocot habit, as for example *Cephalanthera*, with a short rhizome and erect, non-thickened annual stems with scattered, spiral leaves and a terminal inflorescence. The origin of the majority of other sympodial growth forms by phyletic shortening and/or thickening of the stems is readily envisioned. Of special interest is the monopodial habit, in which the stem has unlimited apical growth and roots are not restricted to the basal portion. In some systems this has been considered to be the distinguishing mark of the Sarcanthinae. We find, however, that the monopodial habit occurs in the Vanillinae, Cymbidiinae, Maxillariinae, Pachyphyllinae, Cryptocentrinae, Thelasiinae and Oncidiinae, and possibly in other groups as well. In some of these groups we have a good graded series from sympodial plants to related monopodial types. Not only does the monopodial habit appear to have evolved independently in many groups, but its evolution seems to have followed somewhat different patterns in different cases. In the Vanillinae and the Sarcanthinae it has apparently been the simple retention of apical growth in the members of a sympodium (with lateral inflorescence). In some of the Maxillariinae and allied groups it appears to be the suppression of pseudobulbs on a leafy rhizome. In other cases, such as *Maxillaria valenzuelana*, and some Oncidiinae (*Oncidium pusillum* complex, *Rodriguezia* spp.), the monopodial habit

apparatus to be simpler than in the related *Oreorchis* and *Tipularia*. In the absence of these closely allied genera, its relationship to the Cyrtopodiinae would be much less clear. The saprophytes are difficult to cultivate and poorly represented by herbarium specimens, which further complicates their study. Autogamy is frequent, and an autogamous saprophyte is nearly the ultimate in taxonomic difficulty. A special key to the saprophytic genera of orchids is needed.

PSEUDOBULBS AND CORMS

A great many orchids, and especially the epiphytic groups, show variously thickened stems or "pseudobulbs." While these structures are quite diverse in form, they fall into a limited number of morphological types and seem to show some evolutionary trends. One of these seeming trends is from pseudobulbs (or corms) of several or many internodes to pseudobulbs of a single internode (as in *Bulbophyllum*, Maxillariinae and Oncidiinae). Reference to the chart of relationships (fig. 1) suggests that there may be two basic patterns for the origin of pseudobulbs. In the majority of the Blettiinae, Cyrtopodiinae and related groups (the right side of fig. 1), pseudobulbs seem to have been derived phyletically from more or less corm-like structures, as in *Bletia* and *Phajus*. These thickened stem-bases may be found in either terrestrial or epiphytic groups, while the pseudobulbs of a single internode are restricted to primarily epiphytic groups. The other main pattern for the derivation of pseudobulbs appears to be shown by the Epidendrinae and some related groups (left side of fig. 1). In these groups corm-like structures are not found, and the pseudobulbs appear to have evolved by a phyletic thickening of the entire aerial shoot (as in *Dendrobium*, *Barkeria*, etc.). The more derived members of these groups may also possess pseudobulbs of a single internode, which are morphologically indistinguishable from those of the Oncidiinae or Maxillariinae (ex. *Bulbophyllum*, some species of *Dendrobium*).

LEAVES

The evolutionary trends in leaf type seem rather clear, and have already been outlined by Rolfe (1909-1912). The primitive type of orchid leaf is probably non-articulate, wide (more or less elliptic) and plicate, of convolute vernation. The trends toward an articulate leaf which is narrow (more or less ligulate) and conduplicate, have probably occurred independently in several phyletic lines, and appear to be strongly correlated with the epiphytic habit. It is interesting that the monopodial orchids all have strictly conduplicate leaves, with the partial exception of *Vanilla*, which has convolute vernation, but the fleshy leaves of *Vanilla* are by no means plicate, and the mature leaf usually appears conduplicate. This points out the imperfect correlation between conduplicate leaves and duplicate vernation. The correlation is generally good, however. We have used plicate and conduplicate in the present paper, as terms descriptive of the mature leaf and therefore more readily determined. There are, of course, transitional stages, such as the many-veined but conduplicate leaves of most Cymbidiinae, which appear superficially plicate.

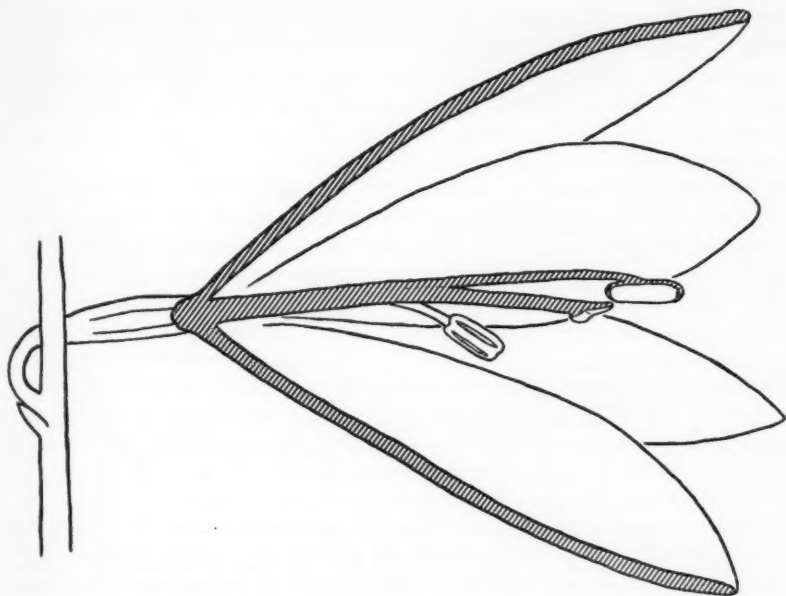


Figure 2. A longitudinal section of a hypothetical primitive orchid flower, highly schematic. In such a flower we would expect the perianth segments to be similar, and we would expect 3 anthers, one of which is borne above the stigma, the other two being lateral in position. Such a flower is closely matched in the living Apostasiae. A simple form of resupination is shown.

FLOWER

It is probable that the primitive orchid flower was a relatively unspecialized monocot flower with equal and similar perianth parts, similar to that now found in the Apostasiae. Such a hypothetical primitive orchid flower is sketched in fig. 2. The only unusual feature of the simpler orchid flowers is a certain degree of zygomorphy in the androecium. The three anthers which are found in the orchids are all on the abaxial side of the flower and are members of two different whorls. The adaxial stamens were evidently lost at an early stage in orchid evolution. In some groups of ancestral orchids, as in the living *Cephalanthera*, the viscid matter of the relatively unspecialized stigma may have served to glue the pollen masses of the median anther to the pollinating agent on its withdrawal from the flower. Such a relationship was surely the basis for the evolution of those tribes in which only the median anther is functional. A tremendous diversity exists in the form of the column and anther among living orchids. So great is this diversity in form and position that it is very difficult to use a precise terminology for the anther and its parts. The column itself has clear dorsal, ventral and lateral aspects (though morphologically confused by resupination, in which the adaxial side of the flower becomes ventral).

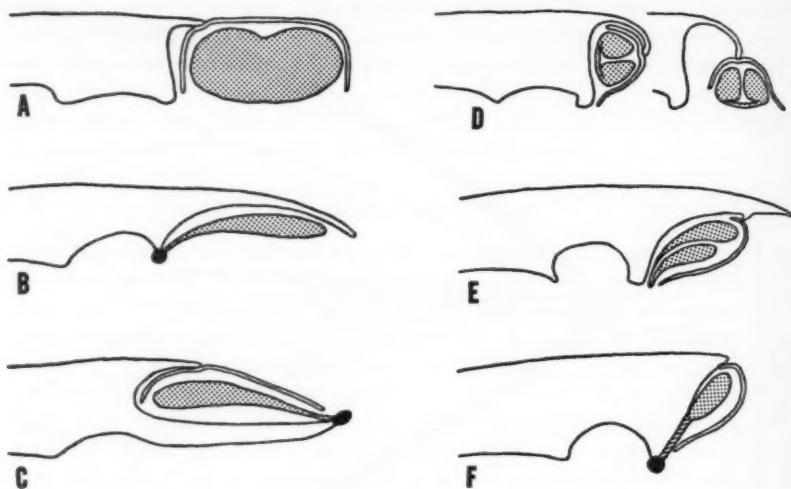


Figure 3. Diagrammatic longitudinal sections of orchid columns, showing the relationships of anther, pollen and stigma. Pollen is stippled; the viscidium, where present, is shown in black. A. A primitive orchid with the anther terminal and erect, the stigma is undifferentiated; *Cephalanthera*. B. A member of the Orchidinae, in which the anther is erect and broadly united to the column. The viscidium (or viscidia) is attached to the base of the pollinia. C. An orchid with dorsal anther; the rostellum is elongate and erect, with the viscidium attached to the apex of the pollinia; *Spiranthinae*, *Meiracyllium*, *Podochilus*, etc. D. An orchid with operculate, versatile anther; *Dendrobium*, *Cattleya*, *Vanilla*, etc. E. An orchid with ventral anther overtopped by the column, as in *Coelogyne*. F. An orchid with a more or less operculate anther and a distinct stipe (cross-hatched) attaching the pollinia to the viscidium. Typical of *Sarcanthinae*, *Maxillariinae*, *Oncidiinae*, etc.

ANTHER

In the subfamily Cyripedioideae three distinct stamens are usually present, though the median anther is represented by a staminode in *Apostasia* and the Cyripedioideae. In the Orchidoideae it is only the median anther which is functional, the lateral anthers being completely absent or represented by staminodia. Three fertile anthers do occur as an occasional abnormality, and are the rule in a few autogamous forms. Vermeulen considers the auricles of *Cephalanthera*, *Epipactis* and the Orchidoideae not to be staminodia. Some other orchids, however, do bear distinct lateral staminodia. *Diuris* is probably the most noteworthy case, for here the staminodia are nearly as long as the style and are free nearly to their bases. Column wings or stielidia occur in a number of genera and are probably staminodia.

It is quite probable that the anther is primitively erect, and the anther is erect in the majority of living Neottieae. In the *Spiranthinae*, *Diuridinae* and related subtribes the anther is dorsal, and does not appreciably overtop the apex of the stigma. In these groups the pollinia are associated with the stigma by a terminal rostellum, and it may be that the dorsal anther is primitive for these groups. In this feature they are quite comparable to some of the *Apostasiae*. In the remaining

Neottiae the anther is normally terminal, usually reaching well beyond the stigma. Thus it is the basal or ventral portion of the pollinia which is usually associated with the rostellum in these subtribes. Such a condition was the probable starting point for the evolution of the Orchideae, for in this tribe the pollinia are attached to the viscidia by basal caudicles. In some members of this tribe the anther is erect and the anther cells fairly close together, the pollinia attaching to a single viscidium or two adjacent viscidia. This is, if not the primitive condition for the tribe, certainly the one most readily understood. In many members of the Orchidinae and Coryciinae the anther cells are widely separated and each pollinium is attached to a separate viscidium, the viscidia often being widely removed from the functional stigma. In the Disinae the anther is usually reclinate, being "bent" backwards from the column. In most species of *Satyrium* the anther actually has the base uppermost.

In the primitive Epidendreae the anther is normally incumbent and operculate on the apex of the column. In these subtribes the anther is actually more or less versatile, the (morphologically) ventral face of the anther resting against the apex of the column until the anther is rotated on the filament, as shown in fig. 3D. The anther is erect in the early floral ontogeny of these groups, and is erect in the mature flower of a few species. This probably represents an ontogenetic "reversion" in these plants, rather than a primitively erect condition, for they are all closely allied to species with fully incumbent anthers. In the more derived members of the Epidendreae the anther may take on almost any position: dorsal, terminal, ventral, or intermediate conditions which render accurate description and categorization difficult (see fig. 3).

ROSTELLUM

The rostellum has been given as one of the family characteristics of the Orchidaceae. In its extreme development it is quite comparable to the situation in the Asclepiadaceae, in which part of the stigma has become associated with the pollen and takes part in the transfer of the pollen from anther to functional stigma. One finds, however, a complete series of gradations in the living orchids from forms with no structure which can be called a rostellum to the markedly complex structures in the advanced Oncidiinae and Sarcanthinae. The rostellum may perhaps be best defined as the structure separating the functional stigma from the anther, a portion of which serves to attach the pollinia to the pollinating agent. It is frequently stated to be the third (median) lobe of the stigma. As Vermeulen (1959) has shown, however, many orchids with a distinct rostellum have three stigma lobes, and the work of Wolf (1866) shows portions of the median lobe to be functionally stigmatic. Indeed, superficial observations suggest that the third stigma lobe may often be much the largest of the three. It would appear that only a portion of the third stigma lobe is involved in the rostellum, and it is not clear that other structures (such as style or filament) are not also involved. In the more highly evolved Orchidaceae the column behaves as a separate organ *sui generis*, the boundaries between the phyletically component parts being lost or

obscured. Vermeulen (1959) believes the rostellum of the Orchideae to be different in origin and nature from that of the Neottieae and Epidendreae, and suggests that it may be derived from the lateral stigma lobes. This does not seem to be supported by the developmental studies of Wolf (1866).

In its most primitive expression, in *Cephalanthera*, the entire stigma is functional as such, and the pollinia are normally attached to insects by a portion of the stigmatic fluid which the insects receive by brushing the stigma in retreating from the flower. In many groups of orchids a special part of the stigma is differentiated to supply the viscid material which attaches the pollinia to the pollinating agent, but the transfer is similar to that in *Cephalanthera*. In *Cattleya*, for example, the rostellum projects beyond the stigma, but the viscid matter and the pollinia do not come into actual contact without action of the pollinating agent. A slight further specialization is seen in *Sophranitis* and some species of *Calanthe*, where a portion of the rostellum is more or less differentiated as a viscid pad which is attached to the pollinia and is removed with them as a unit. This structure is variously known as viscidium, viscid disk or gland; we use the first term, as the structure is not a gland in the usual sense, nor is it usually a disk. In the more highly specialized groups, the viscidium is a sharply delimited structure attached to the pollinia by a strap of rostellar (or columnar) tissue which is not viscid. This connecting tissue is termed the stipe, and is cellular in structure, unlike the translator of the asclepiads. The high degree of diversity in rostellar structure, and the degrees of specialization within taxa suggest that, after the initial action of stigmatic fluid in transfer of pollen, all of the other specializations (viscidium and stipe) have arisen independently several or many times in separate phyletic lines. Early stages in the independent evolution of the viscidium are to be seen in several genera of the Epidendrinae, and the stipe appears to have evolved independently in the Prasophyllinae, Genyorchidinae, Spiranthinae, and perhaps elsewhere.

POLLINIA

The major systems of orchid classification have focused attention on variation in the pollen and associated features. As in most other features, there is a high degree of diversity in the structure of the pollinia, but this diversity is accompanied by many gradations to a simple and unspecialized pollen. The simplest and surely most primitive condition is that in the Apostasiae. In this tribe we find unspecialized 4-locular anthers with powdery pollen. In the Cyripedieae the pollen grains are not united into larger units, but the pollen is somewhat viscid. In almost all members of the Neottieae and Orchideae the pollen grains are united into tetrads (free grains occur in *Cephalanthera*). Further, this granular pollen is usually loosely united into large masses by elastic threads of tapetal origin. These masses, or pollinia, may be two in number, each representing the contents of one half of the anther; more commonly the two halves are each more or less divided, so that each of four anther cells contains a pollen mass. The pollinia of the Orchideae are divided into many granular packets, interconnected by elastic threads. This is the condition termed sectile. In the Neottieae the pollinia are sectile only in the *Good-*

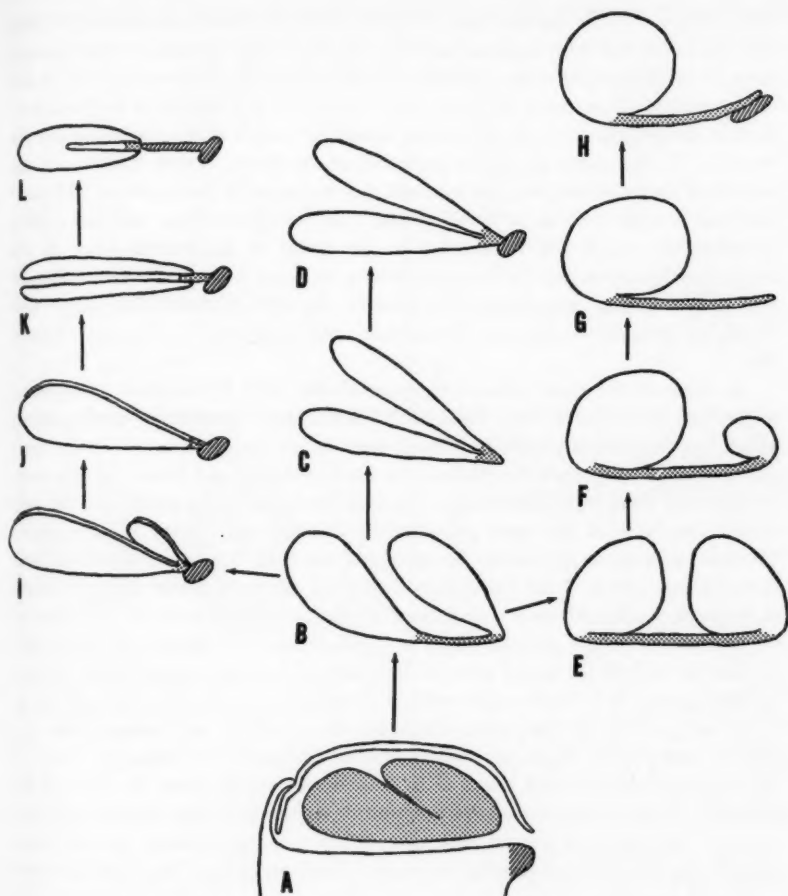
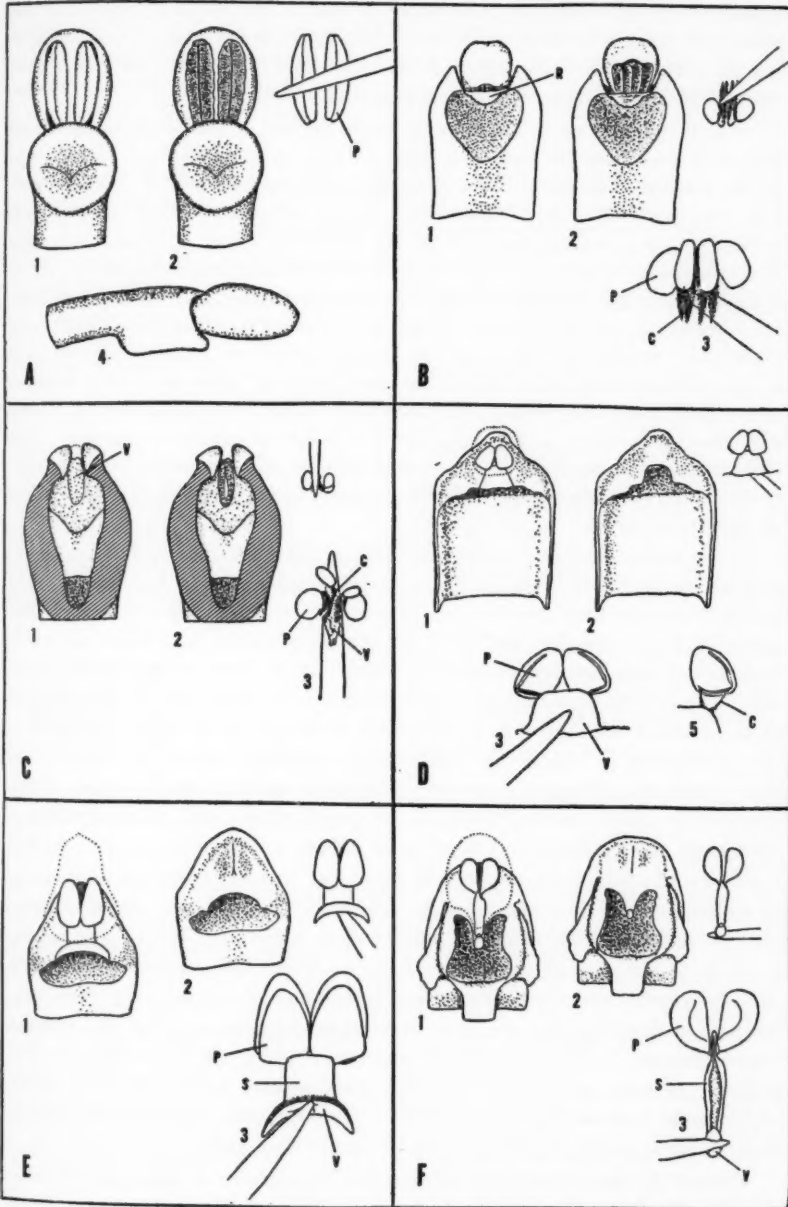


Figure 4. Diagram showing some of the major patterns of evolution in pollinia within the Epidendreae. Mealy pollen (only the caudicles in the higher forms) is stippled; the rostellum in A and the viscidium, where present, are cross-hatched. A. A relatively primitive orchid as in the Arethuseae or Sobraliinae, showing the orientation of the pollen within the anther and the position of the rostellum. In such an orchid there are 4 mealy pollinia, each more or less divided into 2 portions. Highly schematic. B-D. The evolution of clavate pollinia, as in Blettiinae and some sections of *Eria*. A viscidium may be formed (D). E-H. The major pattern of evolution in the *Epidendrum* and *Polystachya* alliances, in which 8 equal pollinia are reduced to 4 (rarely 2). A viscidium may be formed, but is usually attached to the pollinia by caudicles. I-L. The evolution of superposed pollinia, as in Cyrtopodiinae, Sarcanthinae, Maxillariinae and Oncidiinae. In the highly evolved forms the pollinia are frequently reduced to 2 in number and are attached to the viscidium by a stipe.

yera alliance. Sectile pollinia have, by some, been considered an intermediate step between mealy and waxy pollinia, but they represent rather a separate specialization. A single sectile pollinium may pollinate a number of separate flowers, as only a few of the packets are normally left in any one flower. In the Orchideae the basal portions of the pollinia form slender, sterile "caudicles" which attach the pollinia to the viscidia. The caudicles are largely composed of the elastic strands which unite the tetrads of the pollinium, but some tetrads may be found in the caudicles. Distinct caudicles are not formed in the Neottieae. In the Spiranthinae and some other subtribes the viscid disk is attached to the apices of the pollinia, but in the Australian Neottieae one finds a complete series from basal attachment through ventral to terminal attachment like that of the Spiranthinae. The distinction which has been drawn between "Acrotonae" and "Basitonae" is thus an artificial one.

In some of the more primitive groups of the tribe Epidendreae (Vanillinae, Pogoniinae, Arethusinae, some Bletiinae and Sobraliinae) granular or mealy pollinia occur, but the pollinia usually form hard, more or less "waxy" masses. In the more highly specialized groups the pollinia are quite compact and hard. In the Arethusinae and some Sobraliinae each of the four mealy pollinia is partly divided into halves. In most of the more primitive Epidendreae eight waxy pollinia occur. These are subclavate or laterally flattened and occur in two series, each basal pollinium being united to the terminal pollinium of the same anther cell by a band of granular pollinia which is strengthened by elastic strands, as in the caudicles of the Orchideae. These granular bands or caudicles may be united with each other so that the pollinia form two units of four each or a single unit of eight pollinia. In these groups it is the caudicle which is normally attached to the pollinating agent and provides a weak zone which can be stretched and broken when the pollinia contact the stigma of another flower. Reference is frequently made to "a caudicle having a viscid apex" or to "viscid disk arising from the apex of the pollinia." Such statements seem to represent translations from Schlechter's key (1926). As nearly as we can determine, adhesive matter is never derived from the pollinia, but is always rostellar in origin. Bentham (1881) restricted the term

Figure 5. Examples of pollen apparatus found in the orchids. 1. The underside or apex of the column showing the stigma, and the pollinia in place within the anther. The anther is shown by dotted lines in C-F. 2. Same with the pollinia removed by a needle (to the upper right). 3. An enlarged view of the pollinia. c: caudicle; p: pollinia; r: rostellum; s: stipe; v: viscidium. A. *Cephalanthera rubra*: the anther is terminal and erect. Stigmatic fluid serves to attach the pollinia to insects, but no rostellum is differentiated. The pollinia are mealy. 4. Lateral view of column. B. *Cattleya aurantiaca*: the anther is operculate and versatile. A part of the stigma is specialized as the rostellum, but there is no direct connection between the pollinia and the rostellum. Well developed caudicles are present. C. *Epidendrum schlechterianum*: the anther is dorsal (and scarcely visible from beneath). A distinct, though semi-liquid viscidium is formed, and is attached directly to the caudicles of the pollinia. D. *Cymbidium lowianum*: a well developed viscidium is present, but no stipe. The four superposed pollinia are united into two. 5. pollinium slightly separated from viscidium to show the stretched caudicle. E. *Maxillaria elatior*: a short stipe is present but is not sharply differentiated from the viscidium. The four pollinia are superposed. F. *Oncidium anthocrene (powellii)*: a long stipe is present and sharply differentiated from the viscidium (the stipe is translucent at the point of attachment). This last represents a highly evolved pollen apparatus comparable to the structure found in *Asclepias*. All drawn from living material, except A, which is semi-diagrammatic and adapted from Godfrey (1933) and Reichenbach (1851). A: ca. 5.5X. B, C & F: ca. 4.5X & 9X. D: ca. 2X & 3.5X. E: ca. 3.5X & 6.5X.



caudicle to the tribe Orchideae, and used "appendage" for the mealy portion of the pollinia of the Epidendreae. This distinction is taxonomic rather than morphological, and generally has not been followed by other botanists. There is a clear morphological distinction, though, between stipe and caudicle.

Several trends of specialization occur in the pollinia of the Epidendreae, and all may be derived from the subclavate pattern found in many Bletiinae (see fig. 4). In the Pleurothallidinae, *Glomera*, *Podochilus* and some sections of *Eria*, the pollinia are strongly clavate. Within these groups reduction to four or even two pollinia occurs in several cases (ex. in the Pleurothallidinae). Viscidia are relatively frequent (*Glomera*, *Podochilus*, some Pleurothallidinae, *Meiracyllium*, etc.). Stipe-like structures are found in the *Podochilus* alliance, but these may be caudicular in nature, as are those of the Thelasiinae, according to Mansfeld (1937b). In *Dendrobium* and *Bulbophyllum* the four pollinia (which are probably derived from a clavate pattern) are quite naked; the versatile anther, however, is well designed to bring the pollinia in contact with the rostellar adhesive. In the Genyorchidinae and Thecostelinae both a viscidium and a stipe-like structure are formed. The close affinity of *Bulbophyllum* suggests that the Genyorchidinae may lack caudicles. If this is the case, the pollinia must be attached to the viscidium by true stipes, as they appear to be.

In the *Epidendrum* and *Polystachya* alliances, some Bletiinae, and some sections of *Eria*, the pollinia are laterally flattened and usually more or less discoid. The primitive pattern here appears to be that found in *Laelia*, *Brassavola*, and some species of *Bletia*. In these genera the pollinia are relatively discoid, and each pair is connected by a conspicuous caudicle, which may be about as long as the anther cell. The simplest modification of this pattern is the reduction or complete loss of the terminal pollinium in each set. Thus the pattern of *Cattleya*, *Epidendrum*, etc. is achieved, in which only four laterally flattened pollinia are formed. In these genera each pollinium bears a well developed caudicle which projects downward to the vicinity of the rostellum. In several genera, such as *Neobenthamia*, *Sophranitis* and *Epidendrum*, a small or ill-defined viscidium is formed, which is attached to the pollinia by means of the caudicles. In *Polystachya* and some species of *Epidendrum* the viscidium is quite well developed. In some species of *Polystachya*, such as *P. masayensis*, a distinct stipe is formed. Some other species, however, lack a stipe, and the close affinity of *Stolzia* and *Neobenthamia* clearly align *Polystachya* with the Epidendrinae. Reduction or fusion to two pollinia is infrequent in this series, but occurs in *Epidanthus* and some species of *Polystachya*. Also infrequent is the formation of superposed rather than laterally flattened pollinia. In some species of *Polystachya*, there appears to be a phyletic torsion which could lead to superposed pollinia. Semi-spherical, non-flattened pollinia occur in some species of *Epidendrum* and closely allied genera.

One of the most important trends is the development of superposed (rather than laterally flattened) pollinia, which are usually attached to a viscidium. While we have suggested that this pattern might be derived from the clavate pattern, further study is needed. The Collabiinae and Coelogyninae would seem to be

especially critical in this respect. Fusion of the four pollinia into two is common in this pattern. Holttum has suggested that division of two into four may occur in the Sarcanthinae. The fusion into four is frequently imperfect, and it is not unlikely that the trend may be reversed in some groups. Superposed pollinia are

PRIMITIVE	ADVANCED
Roots fleshy, without velamen	Roots spongy, with velamen
Rhizome slender, subterranean	Rhizome fleshy, epiphytic, or absent
Growth sympodial	Growth monopodial
Stem slender, elongate	Stem fleshy, or otherwise modified
Corms or pseudobulbs of many internodes	Pseudobulbs of a single internode
Leaves many, scattered, spiral	Leaves few, clustered or distichous
Leaves plicate	Leaves conduplicate
Leaves non-articulate, persistent	Leaves articulate, deciduous
Leaves herbaceous or leathery	Leaves fleshy
Inflorescence terminal	Inflorescence lateral
Lip similar to the other petals	Lip variously modified, unlike the petals
Flower without a spur	Flower with a spur or spurs
Filaments and style only partially united	Filaments and style completely united
Lateral anthers present and fertile	Lateral anthers staminodia or absent
Anther erect	Anther incumbent, or otherwise modified
Pollen soft, granular	Pollen variously united into pollinia, hard
8 waxy pollinia	Pollinia 6, 4 or 2
Rostellum absent, or simple, without a viscidium	A clearly defined portion of the rostellum (viscidium) removed with the pollinia
Pollinia without a distinct rostellar stipe	Pollinia with a distinct stipe
Ovary 3-celled	Ovary 1-celled
Seed with endosperm	Seed without endosperm
Seed with a wing or sclerotic testa	Seed with thin, reticulate coat

A chart comparing some of the primitive and advanced features to be found among the living orchids. A number of other specializations, such as saprophytism, sensitive anther, united sepals, etc., could be added. In some cases generally primitive features, such as non-articulate leaves or a simple lip, may occur among highly specialized groups. These features are not necessarily primitive in such cases, but may be secondary modifications. Some features are taken from Swamy (1949).

nearly always accompanied by a distinct viscidium (not so in *Coelogyne*). In the majority of genera from the Cyrtopodiinae to the Oncidiinae (as listed on p. 29), the rostellar tissues are differentiated into a distinct stipe which connects the viscidium to the pollinia. In *Cymbidium* and some Cyrtopodiinae and Maxillariinae, however, the stipe is absent or very small, so that it is difficult to separate the "Vandae" on the basis of the stipe alone. The stipe may be partially or completely divided into two, as in *Dipodium* or some species of *Angraecum*. Even when a distinct stipe is present in these genera, it is usually connected to the pollinia by small caudicles. In *Oncidium*, *Cymbidium*, and others, the caudicle is concealed within the furrow formed by the incomplete fusion of the pollinia, and is readily seen only when stretched (fig. 5D).

TRIBAL RELATIONSHIPS AND PHYLOGENY

With the possible exception of the Neottieae, the currently recognized tribes of orchids are relatively natural groups, whose genera are closely knit by clear interrelationships. The relationships between the tribes are less obvious; divergence and extinction apparently have been more important at this level. This is not to imply that the relationships between the tribes are extremely distant. The resemblances between *Tropidia*, *Apostasia*, *Palmorchis*, *Selenipedium* and *Cephalanthera* are strong enough that one may seriously doubt the advisability of distinguishing subfamilies within the Orchidaceae.

The relative advancement of the orchid tribes and their presumed relationships are schematically shown in figure 6. Since the relationships within the Neottieae are not altogether clear, we have diagrammed four different groups of this tribe separately. These are the groups as listed on p. 29. The Neottinae and Spiranthinae are each treated separately, while the Diuridinae, Cryptostylidinae and Prasophyllinae are treated as one series of interrelated subtribes, and the remaining subtribes are grouped with the Limodorinae.

None of the living tribes of orchids could readily be derived from another living tribe, but their derivation from similar or common ancestors is easily visualized. The Cyripedieae are not very closely related to any other group, their relationship to the Limodorinae being perhaps quite as marked as their few resemblances to the Apostasiae. The ladyslippers have clearly diverged early from the main lines of orchid evolution. The Apostasiae more nearly approach the hypothetical ancestral type, the median anther being functional in *Neuwiedia*. They, too, represent a small relic group of somewhat isolated phyletic position, though perhaps closer to the other orchids than are the Cyripedieae. The Orchideae are presumably derived from somewhat *Cephalanthera*-like types, but they would stand quite isolated if it were not for the relic Epigoniinae, which show some relationships to both the Neottieae and the Epidendreae. The Epidendreae might be derived from somewhat Neottieae-like ancestors, but they show more primitive seed structure in the Vanillinae than any living Neottieae, and the two tribes have apparently diverged at an early level in orchid evolution. The subtribes of Neottieae which we group with the Limodorinae are among the more generalized and

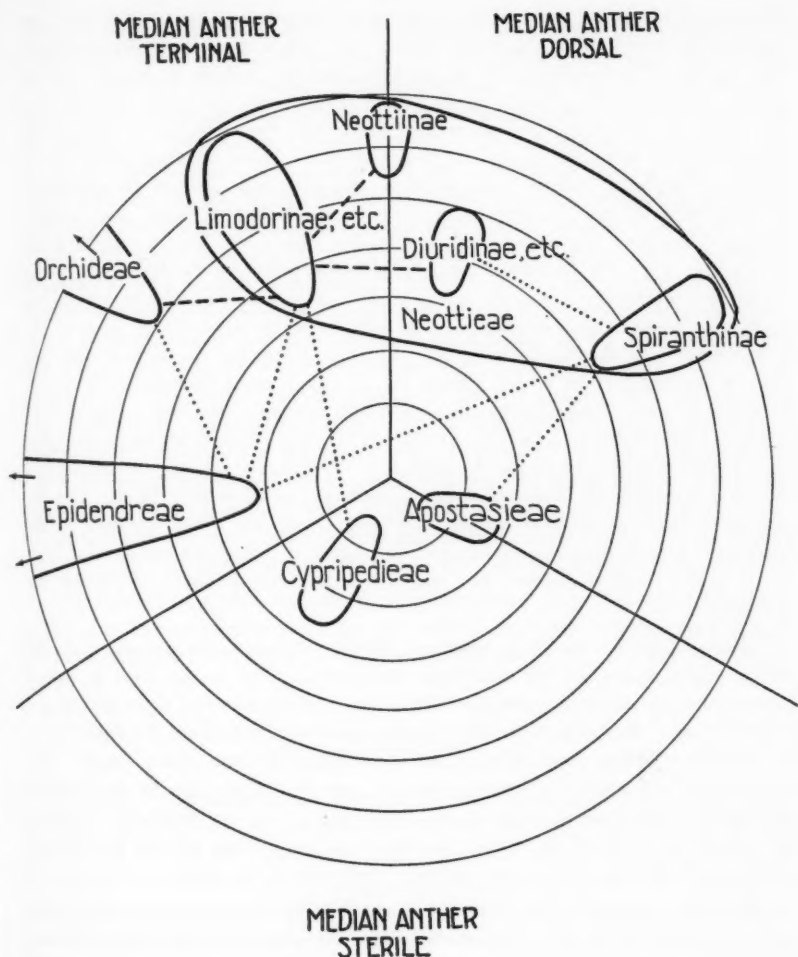


Figure 6. Relative advancement and suggested relationships among the orchid tribes. The less advanced groups have their bases nearer the center, and the ancestral type would fall within the central circle. A more complex advancement index would exclude the Cypripedieae from this sector. Dashed lines are meant to represent closer or more obvious relationships than dotted lines. The subtribes Neottiinae and Spiranthinae of the Neottieae are shown separately; the subtribes Diuridinae, Cryptostylidinae and Prasophyllinae are grouped together, while the remaining subtribes are grouped with the Limodorinae. The advancement index is calculated as follows: lateral anthers fertile, column incompletely formed, anther erect, pollinia mealy, ovary 3-celled, and seed with sclerotic coat or wing; each 0. lateral staminodia present, a distinct column formed, anther incumbent or reclinate, pollinia sectile or ceraceous, ovary 1-celled, and seed coat thin and reticulate; each 1 point. lateral stamens completely absent; 2 points.

primitive of the living orchids, and would be a typically relic group if it were not for the great evolution of this group in Australia, where several striking specializations occur. The association of the rostellum and the pollinia is usually basal or ventral (to the pollinia) in this group, but it is subterminal or quite terminal in a few cases. In the genus *Tbelymitra* one finds a series from clearly ventral viscidia to some species with the viscidium quite terminal. There are some resemblances between *Tbelymitra* and the Prasophyllinae, and these may indicate the derivation of the Prasophyllinae, Diuridinae, etc. from forms with a terminal, erect anther. On the other hand, the conspicuous, nearly free staminodia, and the slight union of filament and style in *Diuris* suggests a highly primitive condition not to be found in *Chloraea*- or *Caladenia*-like plants. The position of the anther in the Neottiiinae is somewhat variable, but this subtribe seems most closely allied to the Limodorinae. In the Spiranthinae the anther is distinctly dorsal and does not overtop the stigma. In several genera the column is more theoretical than real, the short filament being only basally attached to the style (see, for example, Vermeulen's recent figure of *Goodyera*, 1959 p. 339). The *Tropidia* alliance, especially, bears a close resemblance to the Apostasiae. *Tropidia* has actually been described as a new genus of the Apostasiae by Gagnepain (see Mansfeld, 1934). In the absence of clear relationships between the Spiranthinae and other subtribes of the Neottieae, their position is unclear, and it is possible that they are not derived from forms with a terminal anther, but that the anther is primitively dorsal in this group.

The relationships which we suggest between the primitive members of the several orchid tribes are yet somewhat speculative. This is the level at which relationships are expected to be least clear, and, further, many of these orchids are poorly known. We have no detailed morphological information on the Apostasiae, for example. When more information is available on these plants, their inter-relationships will surely be better understood, and we will be able to speculate on their origins with a much firmer basis. While the orchids are unusually favorable for a study of relationships within the family, we may never be able to build an exact and detailed family tree for the early evolution of the group.

We have suggested a change in the circumscription of the Epidendreae, which seems to render the group more natural from the phyletic standpoint and more definable from the descriptive standpoint. In a similar fashion it might possibly be desirable to separate the Spiranthinae as a separate tribe, but further study of this complex is needed. With reference to the subfamily Cypripedioideae, it may be that the Apostasiae should be given subfamilial rank, as Wettstein has already suggested, or it may be that the subfamilial division should be abandoned altogether. Another possibility which must be considered is the recognition of five subfamilies (as Brieger has already suggested, 1958) and the delineation of 10-12 tribes. Such a system might be more comparable to the classifications used for other major families (such as the Compositae and Gramineae).

In dealing with the primitive orchids and their evolution from groups now extinct, we must bear in mind the bewildering parallelisms to be found in the more

advanced groups. If all the monopodial genera with a distinct pollinar stipe were at hand and their sympodial allies extinct, no one could seriously doubt that he was dealing with a "natural" group. The separate and parallel evolution of the different genera of leafless Sarcanthinae would be inconceivable if we did not have the evidence at hand in their living relatives. It is altogether possible that the subfamily Orchidoideae, as now delimited, has not evolved from a single species which possessed all the features of the modern subfamily: column, single fertile anther and rostellum. Rather, this group has probably evolved from a series of related species or genera with partial union of filaments and style, androecial zygomorphy and a close association of the stigma and the median anther; all features which would predispose the group to parallel patterns of evolution. Some of the ancestral populations may have been quite similar to the Apostasiaeae, while others were similar to *Selenipedium*, and yet others quite unlike either. The orchid family is not "unnatural" or polyphyletic in the strict sense, since the ancestral group was, itself, a natural and closely interrelated group, even though it may have differed from the modern orchids in a number of features. We feel fairly sure that the stipe, sectile pollinia and the viscidium have evolved independently in different groups of orchids. It is quite possible that the rostellum, itself, has evolved independently in two or more separate lines and that the reduction to a single median anther is similarly polyphyletic in the unusually "natural" family Orchidaceae.

The patterns of phylogeny and relationships within the orchid tribes help us to understand the evolution of the tribes themselves. A better understanding of both levels may throw more light on the patterns of origin for families and higher categories.

DISCUSSION AND CONCLUSIONS

Probably the foremost conclusion to be reached from a survey of orchid classification is that there are no infallible "key characters." The habit of growth, the presence or absence of pseudobulbs, the nature of the leaves, the position of the inflorescence, the presence or absence of a column foot, the texture of the pollen, the number of pollinia, and the presence or absence of viscidium or stipe; all have been assigned great importance in orchid classification. Yet in every case one can find closely related species which differ in the feature chosen, or even, in some cases, variation within a species. This lack of hard and fast key characters does not mean that a classification of the orchids is impossible. It does mean that a classification must be based on all features of the plant and that comprehensive keys will often be difficult to prepare. Students of the orchids have often erred in assigning too great importance to a single feature. Both our systems of classification and our concepts of relationship are based on relatively few features. With intensive systematic and morphological study we will be able to base our systems on a much broader and firmer foundation.

Ames (quoted by Schweinfurth, 1959) has suggested that many of the difficulties in orchid classification are due to extinction. We feel, on the contrary, that a relative lack of extinction characterizes the family. Interfertility between

morphologically very distinct genera and close morphological resemblances between subtribes, tribes and even subfamilies point to a rapidly evolving group in which extinction has played a minor role. The groups of orchids are closely interrelated, and clear indications of phylogeny are often to be found. Parallelism also plays a part in rendering orchid classification more difficult. There is every indication that monopodial growth, saprophytism, compact pseudobulbs, conduplicate leaves, lateral inflorescences, spurs, viscidia, stipes, and reduction in number of pollinia have all occurred independently in two to several different groups of orchids. It is difficult to define clearly the several groups of monopodial orchids with highly evolved pollinia, yet there appears to be no direct relationship between them. Both classification and phylogeny must be studied by tracing relationships from group to group.

As a family undergoing relatively rapid evolution, the Orchidaceae provide excellent material for the study of evolution. A chart of primitive and advanced features is given on p. 61; a scheme showing the probable relationships between the tribes in fig. 6. There is a tendency to define the family Orchidaceae in terms of its specializations (such as the column, rostellum or pollinia), but one must not lose sight of the primitive features to be found in living orchids. The style and filament are partially free in both the Apostasiae and the Diuridinae; the pollen grains are free in the Vanillinae, and the seeds possess a thick, sclerotic testa in this same subtribe. *Cephalanthera* lacks a rostellum, and several genera bear an erect, relatively unspecialized anther. The patterns of evolution within the family point rather clearly to an ancestor which would be classified in the Lilialean complex of living monocotyledons. Hutchinson has specifically suggested the Hypoxidaceae as a possible close relative of the Orchidaceae. Further morphological study of the primitive orchid genera may greatly clarify this problem. There is no direct relationship between the orchids and the Zingiberales, but rather striking parallelisms, as Hutchinson has suggested. The supposed relationship between the Orchidaceae and Burmanniaceae is based primarily on the tiny seeds; but this type of seed is to be expected in any saprophytic group, and the floral symmetry and inflorescence are basically different in the two groups (Jonker, 1938).

Not only are the fleshy flowers of many orchids crushed in the preparation of herbarium specimens; several of the parts considered important in classification (viscidium, caudicle, pollinia) are frequently dissolved by either alcohol or water. The study of living plants is, thus, especially important. Orchids can, of course, be identified from dried specimens, but a better understanding of relationship is to be obtained from the living plant. Field work by specialists cannot fail to add greatly to our knowledge, while the great variety of orchid genera cultivated by hobbyists can be of great value to botanists.

Finally, we must stress the limitations of the present paper. We have reviewed the nomenclature of orchid tribes and subtribes, following the rules of botanical nomenclature, including priority. We have attempted to evaluate the system of Schlechter, and have offered several changes in arrangement and circumscription, as well as a key to the subtribes which we recognize. We do not consider this a

final, complete system of orchid classification, so much as an evaluation of previous systems, and a working system to be improved and replaced as soon as possible. A discussion of several aspects of orchid phylogeny is presented. Many of the problems which are raised here can best be studied by regional specialists, and it is hoped that the present paper may stimulate such research.

BIBLIOGRAPHY

References marked with an asterisk (*) are those in which new subfamilies, tribes or subtribes are first published.

- *Bentham, G. 1881. Notes on Orchideae. Jour. Linn. Soc. Bot. 18:281-360.
 *Bentham, G. & J. D. Hooker. 1883. Genera Plantarum vol. 3 (Orchideae pp. 460-636).
 *Blume, C. L. 1825. Bijdragen tot de Flora van Nederlandsch Indië 1 (6-8):261-434.
 Brieger, F. C. 1958. On the Phytogeography of Orchids. Proc. 2nd World Orchid Conference 189-200.
 *Brown, R. 1830. Apostasiae in N. Wallich, Plantae Asiaticae Rariores 1:74-76.
 DeWolf, G. P., Jr. 1956. Primary Classification in the Orchidaceae, a Critique. Taxon 5:46-53.
 Duncan, R. E. 1959. Orchids and Cytology, in C. L. Withner, The Orchids, A Scientific Survey, 189-260.
 Finet, M. E.-A. 1896. Sur le Genre *Yosania* Maximowicz. Bull. Soc. Bot. Fr. 43:601-603.
 *Garay, L. A. 1958. Studies in American Orchids IV. Bot. Mus. Leaff. 18:186-218.
 ———. 1959. The Present Status of the Recently Described Genus, *Teuscheria*. Rhodora 61:35-42.
 Godfrey, M. J. 1932. Apostasiaceae. Orchid Rev. 40:355-359.
 ———. 1933. Monograph and Iconograph of Native British Orchidaceae, 259 pp.
 *Hatch, E. D. 1954. Primary Classification in the Orchidaceae. Ceiba 4:222-224.
 Hawkes, A. D. & A. H. Heller. 1959. Phylogenetical Lists of the Orchidaceae. Orchid Weekly 1:261-265, 271-275.
 Holttum, R. E. 1953. Orchids of Malaya. Flora of Malaya, vol. 1, 753 pp.
 ———. 1955. Growth-habits of Monocotyledons—Variations on a Theme. Phytomorphology 5:399-413.
 ———. 1958. Evolutionary Trends in the Sarcanthine Orchids. Proc. 2nd World Orchid Conference 40-48.
 Hutchinson, J. 1959. The Families of Flowering Plants, vol. II Monocotyledons (2nd ed.), 792 pp.
 Jonker, F. P. 1938. A Monograph of the Burmanniaceae. Meded. Bot. Mus. Utrecht 51:1-279.
 *King, G. & R. Pantling. 1898. The Orchids of the Sikkim-Himalaya. Ann. Roy. Bot. Gard Calcutta 8:1-342, pl. 1-448.
 Kränzlín, F. 1923. Orchidaceae-Monandreae-Pseudomonopodiales. Engler, Das Pflanzenreich 83 (IV:50):1-66.
 *Kunth, K. S. 1831. Handbuch der Botanik, 735 pp.
 *Lindley, J. 1826. Orchidearum Sceletos, 22 pp. 3 t. (not seen, copied in Linnaea 2:527-532. 1827).
 ———. 1830-1840. The Genera and Species of Orchidaceous Plants, 553 pp.
 Mansfeld, R. 1934. Orchideologische Mitteilungen. II. Repert Sp. Nov. 36:58-64.
 ———. 1937a. Über das System der Orchidaceae. Blumea, Suppl. 1:25-37.
 ———. 1937b. Über das System der Orchidaceae-Monandreae. Notizblatt Bot. Gart. Mus. Berlin-Dahlem 13:666-676.
 ———. 1954. Über die Verteilung der Merkmale innerhalb der Orchidaceae-Monandreae. Flora 142:65-80.
 Moir, W. W. G. 1959. *Aspasia* and its bigeneric hybrids. Am. Orchid Soc. Bull. 28:431-433.
 *Parlatore, F. 1858. Flora Italiana vol. 3 (Orchidee pp. 333-367).
 Perrier de la Bâthie, H. 1941. Orchidées in H. Humbert, Flore de Madagascar 49 (1 & 2):1-387.
 *Pfitzer, E. 1887. Entwurf einer natürlichen Anordnung der Orchideen, 108 pp.
 ———. 1888-1889. Orchidaceae, in Engler & Prantl, Die Natürlichen Pflanzenfamilien II 4:52-224.
 ———. 1897. Nachtrag zu Orchidaceae, in Engler & Prantl, Die Natürlichen Pflanzenfamilien, Nachtrag und Register zu Teil II-IV: 97-113.
 ———. 1903. Orchidaceae-Pleionandreae. Engler, Das Pflanzenreich 12 (IV:50):1-132.
 Reichenbach, H. G. 1851. Icones Florae Germanicae et Helveticae vol. 14-15 (Orchideae).
 ———. 1852. De Pollinis Orchidearum genesi ac structura et de Orchideis in artem ac systema redigendis, 37 pp. Thesis, Leipzig.

- . 1884. Über das System der Orchideen. Bull. Cong. Int. Bot. Hort. St. Petersburg 39-58.
- Ridley, H. N. 1891. The genus *Brombeesia*. Jour. Linn. Soc. Bot. 28:331-339.
- *Rogers, R. S. 1929. A New Genus of Australian Orchid. Jour. Roy. Soc. W. Austr. 15:1-8.
- Rohrbach, P. 1866. Über den Blütenbau und die Befruchtung von *Epipogium gmelini*. Gekrönte Preisschrift, Göttingen, 28 pp. ill.
- Rolfe, R. A. 1890. A Morphological and Systematic Review of the Apostasiae. Jour. Linn. Soc. Bot. 25:211-243.
- . 1909-1912. The Evolution of the Orchidaceae. Orchid Rev. 17-20 (in parts).
- . 1911. *Phaiocymbidium chardwarens*. Orchid Rev. 19:295-296.
- Schlechter, R. 1911. Die Polychondreae (Neottiinae Pfitz.) und ihre systematische Einteilung. Engl. Bot. Jahrb. 45:375-410.
- . 1915. Nachtrag zu Orchidaceae, in Engler & Prantl, Die Natürlichen Pflanzenfamilien, Ergänzungsheft III:44-61.
- *———. 1926. Das System der Orchidaceen. Notizblatt Bot. Gart. Mus. Berlin-Dahlem 9: 563-591.
- *Schweinfurth, C. 1952. Orchidaceae Peruvianae IX. Bot. Mus. Leaflet. 15:139-170.
- . 1959. Key to the Orchids, in C. L. Withner, The Orchids, A Scientific Survey, 511-528.
- *——— & D. S. Correll. 1940. The Genus *Palmorchis*. Bot. Mus. Leaflet. 8:109-119.
- Smith, J. J. 1934. Artificial Key to the Orchid Genera of the Netherlands Indies, Together with those of New Guinea, the Malay Peninsula and the Philippines. Blumea 1:194-215.
- Sporne, K. R. 1959. On the Phylogenetic Classification of Plants. Am. Jour. Bot. 46:385-394.
- Summerhayes, V. S. 1953. African Orchids. XXI. Kew Bull. 1953:129-162.
- Swamy, B. G. L. 1948. Vascular Anatomy of Orchid Flowers. Bot. Mus. Leaflet. 13:61-95.
- . 1949. Embryological Studies in the Orchidaceae I & II. Am. Midl. Nat. 41:184-232.
- Swartz, O. 1800. Afhandling om Orchidernes Slagter och deras Systematiska indelning. Kongl. Vetenskaps Academiens Nya Handlingar 21:115-138, 202-254.
- Vermeulen, P. 1959. The Different Structure of the Rostellum in Ophrydeae and Neottieae. Acta Bot. Neerl. 8:338-355.
- *Wettstein, R. 1935. Handbuch der Systematischen Botanik, 4th ed., Band II (Angiospermen).
- *Williams, L. O. 1951. The Orchidaceae of Mexico. Ceiba 2:1-321.
- Wolf, T. 1866. Beitrag zur Entwicklungsgeschichte der Orchideen-Blüthe. Jahrb. Wiss. Bot. 4:261-304, ill.

THE GENUS SCHISMATOGLOTTIS (SECTION PHILONOTION) IN AMERICA

GEORGE S. BUNTING

ABSTRACT

The genus *Philonotion* Schott is included in *Schismatoglottis*, forming the American section of an otherwise Asian group. Two species are recognized in this section: 1) *S. americana*, known only from Surinam, and 2) *S. spruceanum*, here transferred from the genus *Philonotion* and represented by two varieties: var. *spruceanum* of Amazonian Venezuela and adjacent Colombia, and var. *williamsii* of Amazonian Venezuela only. GEORGE S. BUNTING, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri.

The genus *Philonotion* was published by Schott (Gen. Aroid. 54. 1858.) to accommodate a single Spruce collection from Amazonian Brazil. For a century, this monotypic genus has been maintained and included in various works on the Araceae. Known from the type collection only, its alliance was variously interpreted. Schott (Prod. Syst. Aroid. 317. 1860.) judiciously placed *Philonotion* in the subtribe Adeloneminae immediately preceding subtribe Schismatoglottidinae. Engler (Pflanzenreich IV. 23(55):24. 1912.) included it in the subtribe Philodendrinae following *Philodendron*. This latter treatment is curious, since that author noted the parietal placentation, the distinctive stamens with apical pores, and the non-scandent habit of growth of *Philonotion*. In contrast, placentation in *Philodendron* is axile, the stamens are of an entirely different nature, and the species are predominantly scandent. The deciduous nature of the blade of the spathe and staminate portion of the inflorescence after anthesis in *Philonotion* further differentiate these two genera.

Philonotion falls clearly into the subtribe Schismatoglottidinae as defined by Engler (l.c. p. 24). Indeed it appears that *Philonotion* is the American section of the otherwise Malaysian genus *Schismatoglottis*.¹ The first and only American species to be described in the latter genus is *S. americana* Jonk. & Jonk. Following its description (Acta Bot. Neer. 2(3):362. 1953.), the authors commented upon the apparent relationship between *Philonotion* and *Schismatoglottis*. The current study has verified the close affinity of these two genera, and has demonstrated clearly that *S. americana* is congeneric with material referred by other workers to *Philonotion*.

Philonotion was initially characterized by a unilocular ovary bearing one parietal ovule. Recent collections that are undoubtedly conspecific with the type of this genus (*P. spruceanum* Schott) have either one or two parietal placentae each bearing one or two ovules, and the unilocular ovary may thus contain one to four ovules. The Malaysian *Schismatoglottis* commonly have ten or more ovules per ovary attached along three parietal placentae. With the exception of the fewer ovules, however, there is no constant floral character separating *Philonotion* from *Schismatoglottis*. Generally, an occasional staminode is found among the pistillate

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¹ Similar disjunction exists in other aroid genera. *Homalomena* is a predominantly Asian genus of about eighty species, six or seven of which occur only in America and have characters diverse enough to be considered as a separate section of the genus by Engler. A similar disjunction occurs in the genus *Arisaema*. One species of the otherwise American genus *Spathiphyllum* is native in Indonesia and the Philippines.

flowers in the latter genus, and some species have a sterile appendage of the spadix. The American species, previously referred to *Philonotion*, exhibit neither of these characteristics, but rather possess one outstanding vegetative feature apparently not found in any Asian species—the aristate or subcaudate apex of the leaf blade. Despite these differences, it seems prudent to reduce *Philonotion* to the rank of section under *Schismatoglottis*.²

SCHISMATOGLOTTIS section *Philonotion* (Schott) Bunt. stat. nov.

Philonotion Schott, Gen. Aroid. t. 54. 1858.

KEY TO THE SPECIES

- A. Leaf blade 2–2.5 times longer than wide, 9 cm. or more wide, elliptic to oblanceolate.
1. *S. AMERICANA*
 AA. Leaf blade narrower, 6 cm. or less wide, lanceolate to oblong.
 B. Blade 3–5 times longer than wide, 2.5–6 cm. wide.....2a. *S. SPRUCEANUM* var. *SPRUCEANUM*
 BB. Blade 7.5–9 times longer than wide, to 1.8 cm. wide.....2b. *S. SPRUCEANUM* var. *WILLIAMSONII*

1. *SCHISMATOGLOTTIS AMERICANA* Jonk. & Jonk. Acta Bot. Neerl. 2(3):360, fig. 2. 1953.

HOLOTYPE: *Maguire 24289*, Tafelberg, Surinam, Aug. 1944 (NY). Known only from the type collection.

2. *SCHISMATOGLOTTIS spruceanum* (Schott) Bunt. comb. nov.

Philonotion spruceanum Schott, Gen. Aroid. t. 54. 1858.

- 2a. *SCHISMATOGLOTTIS SPRUCEANUM* var. *SPRUCEANUM*.

Stenospermantium verecundum R. E. Schultes, Bot. Mus. Leaflet 18(4):121–122, pl. XXI, XXII. 1958.

LECTOTYPE: *Spruce 2948*, in ripis rivuli umbrosi, secus Panuré, Alto Amazonas, Brazil, Feb. 1853 (K). This is a duplicate of the holotype. The latter was deposited at Vienna and presumably destroyed when that herbarium burned following World War II. I have seen only a photograph of the Kew sheet; it appears to be nearly identical to the largest specimen on the New York sheet of *Maguire 36413*.

ADDITIONAL SPECIMENS: *B. Maguire, J. J. Wurdack, & G. S. Bunting 36311*, Yavita-Pimichín trail, Río Guainía, Terr. Amazonas, alt. 120–140 m., Nov. 21, 1953; *36413*, sabanita 1 km. east of Maroa, Río Guainía, Terr. Amazonas, Venezuela, alt. 120–140 m., Nov. 25, 1953; *36415A*, same data as *36413*.

The infrutescence of this variety has not been previously described. It is fusiform, about 3.5 cm. long and to 1.5 cm. in diameter (in the dried specimen), green, the apex more or less truncate (resulting from loss of blade of spathe), the

² To include this section, Engler's description of *Schismatoglottis* (Pflanzenreich IV. 23(55):82. 1912.) is emended as follows: "... placentis 1–4 parietalis e baseos adscendentibus; ovula 1–plura hemianatropa vel hemiamphitropa ...".

free upper margin revolute; fruits many, baccate, oblong, about 3 mm. long, 1 mm. broad, 1(-2)-seeded.

Schultes & Cabrera 17496 (GH), collected along Río Piraparaná, Comisarias del Amazonas & Vaupés, Colombia, appears to belong here. Unfortunately, that specimen could not be located at the time of this study. It is cited as type of *Stenospermantium verecundum*, but the photograph and plate accompanying the description of that species illustrates a plant clearly referable to *Schismatoglottis spruceanum*.

2b. *SCHISMATOGLOTTIS SPRUCEANUM* var. *williamsii* (Steyserm.) Bunt. comb. nov.

Philonotion williamsii Steyserm. Fieldiana Bot. 28(1):99, fig. 14. 1951.

HOLOTYPE: *L. Williams 13922*, Yavita, Terr. Amazonas, Venezuela, alt. 128 m., Jan. 23, 1942 (F).

ADDITIONAL SPECIMENS: *B. Maguire, J. J. Wurdack, & G. S. Bunting 36415B*, sabanita 1 km. east of Maroa, Río Guainía, Terr. Amazonas, Venezuela, alt. 120-140 m., Nov. 25, 1953. This is a mixed collection, *36415A* representing *S. spruceanum* var. *spruceanum*.

This variety appears to grow together with the variety *spruceanum*, but is distinctive in its much narrower leaf blades and slender petioles. Too few specimens have been collected to indicate to what degree these two forms intergrade.

S. spruceanum is a savannah species, occurring in partial sun on white sandy soil. It seems inappropriate to consider these conditions as "extreme xerophytism" as Schultes suggests (Bot. Mus. Leaflet 18(4):122. 1958.). Though the habitat may appear xeric, my field observations at Yavita and Maroa, Venezuela, were that abundant moisture was present about the roots of the plants.

MISCELLANEA TAXONOMICA. II.

ABSTRACT

The following new taxa are described—Amaryllidaceae: *Crinum brevilobatum* G. McCue; Loganiaceae: *Desfontainea costaricensis* Woodson; Apocynaceae: *Aspidosperma limae* Woodson, *Woytkowskia spermatochorda* Woodson, *Tabernaemontana brachyantha* Woodson, *Peltastes ampliflorus* Woodson, *P. peruvianus* Woodson, *P. tubiflorus* Woodson, *Mandevilla sandemanii* Woodson, *Prestonia caudata* Woodson; Asclepiadaceae: *Matelea rivularis* Woodson.

AMARYLLIDACEAE

CRINUM brevilobatum G. McCue, spec. nov.

Bulbus cylindraceus cr. 11.5 cm. longus. Folia 6 lorata acute acuminata 38–48 cm. longa 4.5–5.0 cm. lata stricte erecta nervis 36–46 parallelis in reticulo per venas breves transversas conjunctis margine denticulis minutis inaequalibusque inaequaliter positis. Pedunculus 27–47 cm. longus in statu compresso 2–4 mm. latus; bracteae 2 inter sese liberae paene vaginantes anguste ellipticae 8 cm. longae apice acutae; flores in umbella 2–4 sessiles v. subsessiles. Perianthii tubus 15–17 cm. longus in statu compresso usque 2–4 mm. latus erectus; limbi segmenta elliptico-lanceolata apice acuminata 3.5 cm. longa medio 5 mm. lata colore flos lactis. Stamina segmentis corollae breviora 1.2 longa prope faucem instructa; antherae lineares 1.2 cm. longae sub medio versus affixae. Stylus corolla perpaullo brevior; stigma minutum lobatum. Ovarium 1.2 cm. longum.

COSTA RICA: ALAJUELA: in moist humus at edge of forest along Río Frío, low tropical rainforest with palms prominent, vicinity of Los Chiles, alt. 30–40 m., August 1, 1949, R. W. Holm & H. H. Illis 695 (HOLOTYPE, MO).

This species is referable to subgenus *PLATYASTER* of Baker, but is remarkable for the short perianth segments relative to the greatly elongate tube.

LOGANIACEAE

DESFONTAINEA costaricensis Woodson, spec. nov.

Frutices epiphytici; ramulis usque 1 m. longis crassiusculis subtetragonis valde compressis semper glabris maturitate cortice luteo-brunneo rimoso tectis. Folia opposita; lamina obovata 2–6 cm. longa 1.5–2.5 cm. lata basi anguste cuneata in petiolum 0.5–1.0 cm. longum decurrente supra medium prominente spinosodentata. Flores solitarii ramulos axillares perbreves terminantes; pedicello ca. 1.5 cm. longo; calycis laciniis ovato-ellipticis acutis ca. 6 mm. longis omnino glabris; corollae salverformis tubo paene recto ca. 2 cm. longo basi ca. 2.5 mm. diam. fauces versum paulo ampliato aurantiaco-rubeo, lobis late ovatis ca. 8 mm. longis paulum patulis luteis.

COSTA RICA: CARTAGO: dense virgin cloud-forest, vicinity of Millsville, Pan-American Highway, about 3 km. above Nivel, alt. 3000–3300 m., July 22, 1949, R. W. Holm & H. H. Illis 534 (HOLOTYPE, MO).

An interesting addition to the flora of Central America, this species approaches *D. obovata* Krzl., of Peru, in the small calyx which, however, is ciliate as is usual in

the Andean species. There probably is close relationship also to *D. pulchra* Moldenke, of Venezuela, which, however, has oblanceolate subentire leaves.

APOCYNACEAE

ASPIDOSPERMA limae Woodson, spec. nov.

Arbores altae sicut collector dixit altitudine ignotae laticem sanguineum exudentes; ramulis pro magnitudine graciliusculis glabris vel juventate minutissime papillatis cortice atrofusco arcte compresso. Folia irregulariter approximata longe petiolata; lamina latiuscule elliptica apice valde acuminata basi obtuse cuneata ca. 8–12 cm. longa 3.5–5.0 cm. lata rigide coriacea margine paulo revoluta supra valde illustri colore olivacea venis immersis subtus pallidiore venis vix bene visis utrinque glabra; petiolo 2–4 cm. longo tenui glabro colore ramuli. Inflorescentiae terminales et subterminales manifeste cymosae; ramulis terminalibus quam lateralibus conspicue brevioribus sordide griseo-tomentellis multifloris foliis subaequantibus; bracteis vix bene visis; pedicellis vix 1 mm. longis. Calycis laciniae ovate acutae 2 mm. longae atrogrieco-tomentellae. Corolla luteola extus glabra; tubo valde angulato ca. 3.5 mm. longo 1.5 mm. lato; lobis ca. 3.5 mm. longis valde caudato-acuminatis et spiraliter contortis. Folliculi magni oblique elliptico-ovales apice late obtusi basi in stipitem crassum sensim producti 15–18 cm. longi 8–9 cm. lati dense fuscogrieco-tomentelli; seminibus late ovalibus ca. 8 cm. longis 7 cm. latis.

BRASIL: PERNAMBUCO: Recife, Dois Irmãos, Oct. 4, 1949, Dárdano de A. Lima 49-333 (HOLOTYPE, MO).

This very distinct species of series NOBILES will key in my revision of *Aspidosperma* (Ann. Missouri Bot. Gard. 38:185. 1951) to the alliance of *A. album* and *A. sandwithianum* because of the inflorescences of distinctly cymose aspect (the determinate branches much shorter than the divaricate lateral branches). However, the general aspect of the specimens is much more reminiscent of *A. megalocarpon*, particularly because of the massive densely tomentellous follicles. It is the first species of series NOBILES recorded for Pernambuco. Mr. Lima quotes the popular name of the trees as *pitia marfim* and states that the timber is useful for cabinet work.

Woytkowskia spermatochorda Woodson, gen. et spec. nov. (*Tabernaemontanoideae*)

Frutices mediocres lactescentes. Folia disticha anisophylla; lamina obovato-elliptica abrupte caudato-acuminata basi latiuscule cuneata ca. 9–20 cm. longa 5–9 cm. lata tenue membranacea glabra nervis secundariis in utroque latere 10–16 arcuatis; petiolo 5–12 mm. longo basi paulo amplexantem et in axilla pluriglanduloso. Inflorescentia aut terminalis aut interpetiolaris cymosis subtriflora. Flores gilvi pedicellati; calycis laciniae 5 subaequalibus late ovato-deltoides rotundatis 3–4 mm. longis glabris intus in axillis pluriglandulosis; corollae tubulo-salverformis tubo conico-cylindrico ca. 2.0–2.5 cm. longo basi ca. 4 mm. diam. ostio ca. 1.5 mm. diam extus glabro, lobis 5 ante anthesim in ostium fere omnino inflexis

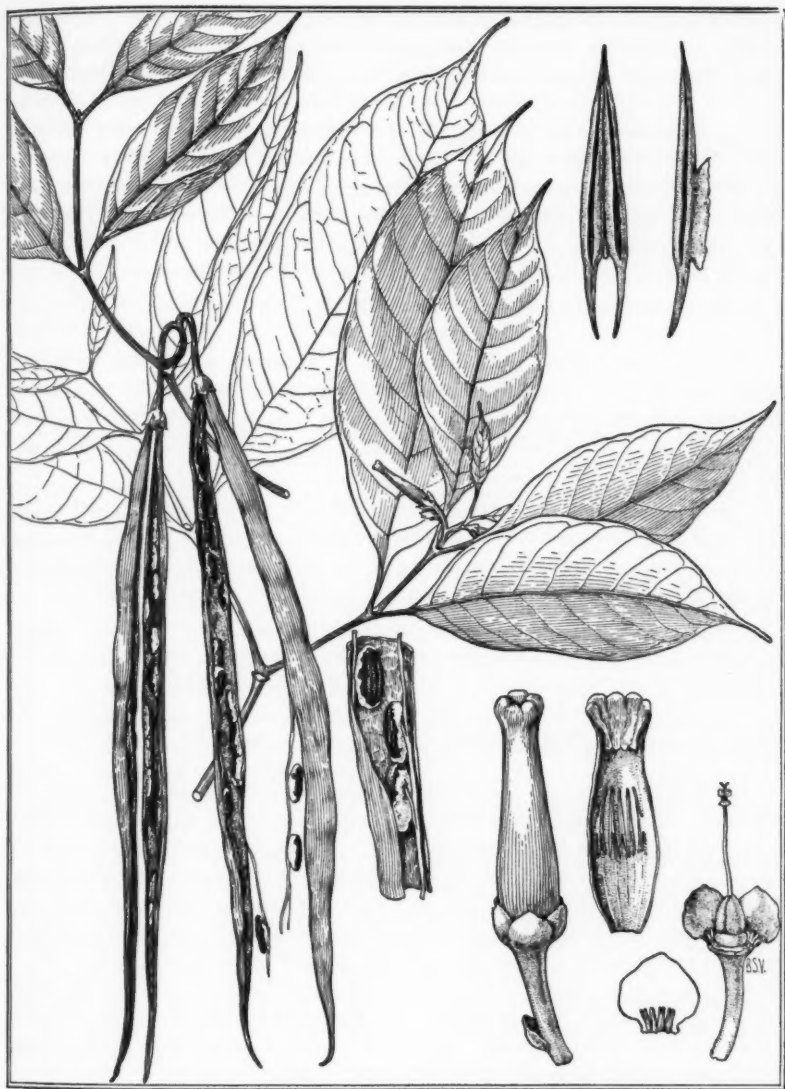


Figure 1. *Woytkowskia spermatochorda* Woodson

(alabastro apice manifeste invaginato) oblique oblongis ca. 5–6 mm. longis; antheris 5 sessilibus anguste sagittato-lanceolatis ca. 11 mm. longis basibus thecarum paulum incurvis angustis sterilibus medio tubo corollae insertis; carpellis pistilli 2 apocarpis oblongo-ovoideo in quoque loculo ovulis multis 2-seriatis, stylo gracili, stigmatibus umbraculiformi parte apicali anguste bifida parte media dilatata subglobosa leviter sulcata basi contracta parte basali limbo brevi reflexo, nectario annulari demisso carnosio subintegro. Folliculi 2 lineari-fusiformes usque 20 cm. longi 5 mm. lati pericarpio sicco tenui extus indistincte striato glabro; seminibus late fusiformibus ca. 8 mm. longis testa fusca profunde striata arillo sicco papyraceo ca. semi-involutis placenta filiformi decidua persistente affixis.

PERU: LORETO: in forest, Aguaytia, alt. 300 m., F. Woytkowski 5338 (HOLOTYPE, MO).

The fruits are utterly unlike those of any *Tabernaemontana* known to me. Whilst the seeds are provided with the aril common to the alliance, here it is dry and not fleshy, being permanently attached to the peculiar filiform deciduous placenta from which the specific substantive is coined. The elongate follicles also are unparalleled in *Tabernaemontanoideae*.

The corolla lobes of *Tabernaemontana* ordinarily are partially included within the throat prior to anthesis; but here they are almost completely inflexed, rendering the tip of the bud decidedly concave. I have only unopened buds available for examination, but assume that the lobes are extruded from the orifice at anthesis.

The specific epithet descriptive of the placenta might be used more strikingly as a generic name, but I feel constrained to commemorate in this way the invaluable botanical contributions of my colleague Félix Woytkowski.

TABERNAEMONTANA brachyantha Woodson, spec. nov.

Frutices altitudine ca. 3 m.; ramulis teretibus fuscis glabris vel indistincte papillatis. Folia disticha subisophylla; lamina late ovato-elliptica subcaudato-acuminata basi obtusa 15–25 cm. longa 5–12 cm. lata membranacea glabra subtus subglauca nervis secundariis in utroque latere 15–20 arcuatis; petiolo 1–2 cm. longo basi paulo amplexantibus et conspicue elevato-mitrato in axilla pluriglanduloso. Inflorescentia aut terminalis aut interpetiolaris dichotome cymosa ca. 20-flora petiolis paulo superans. Flores pro genere parvi albi breviter pedicellati. Calycis laciniae ovate late acutae similes ca. 2 mm. longae minute ciliolatae in axillis squamellis ligularibus 4–6 gerentes. Corollae salverformis extus glabrae tubo cylindrico 9–10 mm. longo basi ca. 1.5 mm. diam. ostio paulo constricto, lobis limbi oblique oblongo-ovatis ca. 4 mm. longis post anthesim patulis in alabastro ca. dimidio inclusis. Antherae sessiles vix inclusae 3 mm. longae caudiculis sterilibus paululo incurvis. Pistilli carpelli ovoideo-fusiformia glabri intus ovulis multis 2-seriatis, stylo gracili, stigmatibus ca. 1 mm. diam. parte apicali minute 2-dentata media oblate 5-gona basali limbo brevi reflexo, nectario 5-lobato adnato demisso. Fructus ignotus.

PERU: LORETO: Aguaytia, in forest, alt. 300 m., May 10, 1959, F. Woytkowski 5345 (HOLOTYPE, MO).

I assume that this is a species of the *Bonafousia*-complex of *Tabernaemontana* (*sensu lato*) but the flowers are far smaller than for those of any other species known to me and furnish a striking contrast to the large leaves. The fruit should be awaited with unusual interest.

I feel that insufficient prominence has been given to the vegetative characters of the *Tabernaemontanoideae*—the dichotomous branching of the stem, the interpetiolar inflorescence, and particularly the inconspicuous prophyll which is the first-borne appendage of each dichotomous branch and by means of which alone the frequent "lateral" inflorescences may be demonstrated as terminal. The very base of the petioles is somewhat amplexant and canaliculate for the protection of the terminal bud, and not infrequently developed into a conspicuously elevated hood, as in this species.

PELTASTES ampliflorus Woodson, spec. nov.

Frutices volubiles; ramulis teretibus crassis juventate minute ferrugineo-papillatis. Folia opposita petiolata; lamina peltata latissime ovata apice abrupte mucronata basi late rotundata 25–30 cm. longa 20–22 cm. lata firmiter membranacea supra glabra subtus pallidiori inconspicue ferrugineo-papillata; petiolo 6–7 cm. longo ferrugineo-tomentello. Inflorescentiae in axillis oppositis foliorum pluriflorae; pedunculis ca. 6–8 cm. longis ferrugineo-tomentellis; pedicellis 1.5–2.0 cm. longis minute ferrugineo-tomentellis. Flores infundibuliformes gilvi extus minute dense ferrugineo-puberuli; calycis laciniis valde inaequalibus interioribus oblongis ca. 1.8 cm. longis exterioribus late ellipticis ca. 2 cm. longis omnibus foliaceis extus dense puberulo-papillatis; corollae tubo proprio ca. 1.5 cm. longo basi ca. 3 mm. diam., faucibus angustissime conicis ca. 4 cm. longis ostio ca. 1.2 cm. diam., lobis late dolabriformibus obtusis ca. 2 cm. longis 1.5 cm. latis patulis; antheris anguste sagittiformibus dorso glabris.

PERU: SAN MARTIN: mountain forest, Zepelacio near Moyobamba, alt. 1100 m., August, 1934, G. Klug 3754 (HOLOTYPE, MO).

I had previously determined this specimen as *P. giganteus*, which cannot be accepted because of its glabrous anthers. It must be very closely related to *P. peruvianus*, but the ferruginous-puberulent corollas of somewhat different shape would appear to preclude that, as well as the larger broader foliage, smaller narrower calyx lobes, etc. The "new species" of *Peltastes* appear to be multiplying alarmingly, due mostly to myself, but the genus is encountered by collectors so infrequently that an adequate evaluation of the infra-specific variation seems impossible at present.

PELTASTES peruvianus Woodson, spec. nov.

Frutices volubiles validi ca. 4–6 m. alti; ramulis teretibus crassiusculis juventate dense ferrugineo-tomentellis. Folia opposita longe petiolata; lamina peltata late ovali apice abrupte breviterque subcaudato-acuminata basi rotundata 20–25 cm. longa 14–16 cm. lata firmiter membranacea supra glabra subtus pallidiorae praecipue in nervis minute ferrugineo-tomentella. Inflorescentiae in axillis oppositis

foliorum pluriflorae; pedunculis ca. 5–6 cm. longis minute tomentellis; pedicellis ca. 2 cm. longis ut in pedunculo vestitis. Flores infundibuliformes gilvi extus glabri; calycis laciniis inaequalibus late ellipticis apice acutis vel obtusis 2.0–2.5 cm. longis 0.8–1.0 cm. latis foliaceis; corollae tubo proprio ca. 1.2 cm. longo basi ca. 3 mm. diam., faucibus subtubiformibus vel angustissime campanulatis ca. 3 cm. longis ostio ca. 1 cm. diam., lobis patulis latissime dolabriformibus apice anguste acutis ca. 2.5 cm. longis et latis; antheris anguste sagittiformibus dorso glabris. Fructus ignoti.

PERU: HUANUCO: on outskirts of forest, alt. 1600 m., Divisoria, Sept. 6, 1946, F. Woytkowski 34492 (HOLOTYPE, MO).

The glabrous anthers ally this species and the preceding with *P. malvaeflorus* of southeastern Brazil and *P. stemmadeniiflorus* of Paraguay, from both of which it is distinguished by the exceedingly short proper tube and the very narrow throat of the corolla. Isotypes may be found labeled as *Macropharynx* in other herbaria.

PELTASTES tubiflorus Woodson, spec. nov.

Frutices volubiles validi; ramulis florigeris crassiusculis teretibus dense minuteque ferrugineo-tomentulosi. Folia basi peltata obovato-ovalia apice breviter cuspidata basi rotundata 15–20 cm. longa 9–12 cm. lata membranacea utrinque dense minuteque ferrugineo-tomentulosa supra glabrata; petiolo 4–5 cm. longo. Inflorescentiae in axillis foliorum binis corymbose fasciculatae pluriflorae omnino minuteque ferrugineo-tomentulosi petiolis breviores. Flores pro genere perparvuli. Calycis lacinae foliaceae late oblongo-lanceolatae acutae ca. 1.5–1.7 cm. longae, squamellis multis dentiformibus. Corolla tubulo-salverformis, tubo 5-gono ca. 1.8 cm. longo basi ca. 3–4 mm. diam. dein paulo ampliato prope medio abrupte constricto ibique staminigero deinde ampliato deinde ad ostium ca. 2 mm. diam. gradatim angustato, lobis patulis oblique ellipticis ca. 1 cm. longis. Anthera sagittata more generis ca. 8 mm. longa dorso glabra. Ovarii carpella late ovoidea ca. 1.5 mm. longa glabra basi nectriis 5 humilibus cincta.

BRASIL: MINAS GERAIS: Fazenda Varginha, 12 km. E. of Ponte Nova, Municipio Ponte Nova, 7 December 1958, H. S. Irwin 2246 (HOLOTYPE, US).

The corolla of all other species is far larger and broadly infundibular. Another *Peltastes* sent me for identification by the U. S. National Herbarium at the same time as the above is *Kublmann 2528* from Viçosa, Minas. It apparently also has small flowers much like those of the Irwin number, but is not in condition for close examination. I hesitate to assign it to *P. tubiflora* because of its definitely ovate leaves with a more minute scarcely ferruginous indument.

MANDEVILLA sandemanii Woodson, spec. nov.

Frutices volubiles vel subvolubiles; ramulis crassiusculis juventate dense fulvo-tomentulosi. Folia opposita breviter petiolata; lamina ovata vel ovato-elliptica apice late acuta minuteque mucronulata basi late cordata ca. 11 cm. longa 5–6 cm. lata membranacea utrinque fulvo-tomentulosa subtus densius nervo medio basi pauciglandulosa; petiolo 1.0–1.5 cm. longo dense tomentuloso. Inflorescentiae

axillares simplice racemosae in holotypo laxae 17-florae; pedunculo 35 cm. longo crassiusculo; pedicellis sat distantibus ca. 3 cm. longis ut in pedunculo minute fulvo-tomentulosis; bracteis minutis vix bene visis. Flores spectabiles; calycis laciniis ovato-lanceolatis anguste acutis 8-9 mm. longis foliaceis conspicue puberulis; corolla infundibuliformis viridi extus glabra, tubo proprio cylindrico ca. 2 cm. longo basi 2 mm. diam., faucibus campanulatis ca. 1.3 cm. longis ostio ca. 1 cm. diam., lobis fere erectis late dolabriformibus minute apiculatis ca. 2.5 cm. longis 1.3 cm. latis; antheris anguste elliptico-oblongis basi truncatis ca. 1 cm. longis dorso glabris; carpellis ovoidio-oblongoideis, ca. 2 mm. longis glabris, nectariis 5 distinctis subquadratis subaequalongis, stigmatibus umbraculiformi conspicue apiculato. Fructus ignoti.

PERU: HUANUCO: Carpath divide, alt. 9000 ft. alt., Oct. 7, 1945, C. Sandeman 5154 (HOLOTYPE, K).

Mandevilla sandemanii is most closely related to *M. albobiridis* which is known only from the type specimen from Colombia. The flowers (as well as the whole inflorescence, for that matter) of the former is very much larger in all respects, however, and the nodes are without the conspicuous coriaceous appendages which distinguish the latter.

PRESTONIA (§ COALITAE) *caudata* Woodson, spec. nov.

Frutices volubiles graciles glaberrimi; ramulis teretibus striatis subglaucescentibus, internodiis elongatis. Folia opposita anguste elliptica acuminata basi obtusa 12-14 cm. longa 4.0-4.5 cm. lata subcoriacea indistincte venosa subtus glaucescentia; petiolo 5-7 mm. longo. Inflorescentia lateralis alternata laxa et ca. 10- vel 16-flora simplice cincinnata; pedunculo ca. 20 cm. longo gracillimo, internodio primario ca. 10 cm. longo; pedicellis ca. 2 cm. longis; bracteis trigonalibus ca. 1 mm. longis. Flores luteoli; calycis laciniis late trigonalibus ca. 1 mm. longis, squamellis oppositis subaequilongis irregulariter laceratis; corolla salverformi, tubo late cylindrico ca. 9 mm. longo medio ca. 2.5 mm. diam. extus glabro intus exappendiculato prope insertionem staminis piloso caeterumque glabro, ostio valde incrassato ibique rubro-tincto dicitur, lobis patulis ca. 1.5 cm. longis prope basim ca. 3 mm. latis deinde abrupte angustaeque caudato-acuminatis et spiraliter contortis; antheris inclusis sessilibus anguste lanceolato-sagittatis basi anguste 2-lobatis ca. 5 mm. longis dorso glabro; carpellis anguste conico-oblongoideis ca. 2 mm. longis glabris, nectariis 5 valde discretis compressis oblongoideis ca. 1 mm. longis; stigmatibus oblongo-fusiformi basi indistincte annulato ca. 1.5 mm. longo.

COSTA RICA: PUNTARENAS: vicinity of Casacajal, Hacienda Sta. Maria 25 km. ESE of Puntarenas, alt. 30-100 m., July 3, 1949, R. W. Holm & H. H. Iltis 243 (HOLOTYPE, MO).

This extremely distinct species comes as a great surprise, since its only close relative is *P. agglutinata* of Hispaniola and Puerto Rico. From the latter *P. caudata* is distinguished very sharply by the very long-pedicellate flowers with the peculiar corolla lobes longer than the tube.

ASCLEPIADACEAE

MATELEA rivularis Woodson, spec. nov.

Suffrutices mediocres 2-4 dm. alti parce ramosi; ramis gracilibus ca. 1 mm. diam. juventate minute appresse pilosulis mox glabris. Folia opposita; lamina lineari-elliptica acuminata 2-5 cm. longa 4-6 mm. lata basi in petiolum ca. 3-5 mm. longum gradatim angustata membranacea utrinque glabra subtus pallidiori. Inflorescentiae subterminales interpetiolares pedunculatae umbelliformes parviflorae; pedunculo 1-2 cm. longo minute appresse pilosulo; pedicellis tenuibus 1.5-2.0 cm. longis ut in pedunculo vestitis; bracteis minutis. Calycis lacinae ovato-deltoidae obtusae ca. 2 mm. longae extus dense pilosulae intus in marginibus 1-glandulosae. Corolla livide brunnea vel rubra rotata ca. 1.5 cm. diam.; lobis ovato-oblongis late acutis 7-8 mm. longis glabris; fauce parce annulato. Corona depresso pentagono-patelliformis ca. 1.5-diam. segmentis 5 majoribus leviter divisus margine humile arcuato intus inconspicue umbonatis cum 5 minoribus obtuse dentatis sequentibus alternatis. Gynostegium subsessile discoideum ca. 1.25 mm. diam. depresso umbonatum; pollinii corpusculo minute sagittato-lineari ca. 0.2 mm. longo, saccis late obovatis cum caudiculo hyalino inciso perbrevis ca. 0.3 mm. longis. Folliculi erecti pedunculo pedicelloque erectis fusiformes ca. 2.5-3.0 cm. longi saepe 1 cm. crassi laeves glabri; seminibus multis parvis rhomboideo-ovalibus suberoso-marginatis ca. 2 mm. longis.

ECUADOR: SANTIAGO-ZAMORA: near Méndez, alt. 1750-2500 ft., uplands along Río Upano just north of junction with R. Chupiantza, Nov. 14, 1944, W. H. Camp E-1006 (HOLOTYPE, MO); Cordillera Cutucú, ca. 20° 40' S., 78° W., on rocks, subject to periodic overflow, covered twice in 10 days, and this the "dry" season, the water with terrific force, Nov. 17-Dec. 5, 1944, Camp E-1211 (NY).

PERU: SAN MARTIN: Cahazuta, Río Hualaga, alt. about 260 m., forest, March, 1935, G. Klug 4036 (MO); Pongo de Cainarachi, Río Cainarachi, tributary of Río Hualaga, alt. about 230 m., forest, Klug 2726 (MO); San Roque, alt. 1350-1500 m., Jan.-Feb., 1930, L. Williams 7724 (MO); Tarapoto, alt. 750 m., December, 1929, Williams 6010 (MO).

The Klug and the Williams specimens doubtless are distributed in many herbaria as "*Acomosperma rivularis* K. Sch.", under which they were received at the Missouri Botanical Garden. As nearly as I can ascertain, this name has been published only as a *nomen nudum* in E. Ule's account of the riparian vegetation of the Cainarachi river (Die Pflanzenformationen des Amazonas-Gebietes II. in Engl. Jahrb. 40:406. 1908). The plants must be rather common in the middle highland drainage of eastern Peru and Ecuador.

The species is a typical *Mateleia* and strikingly parallel to the original element of the genus, *M. latifolia* Aubl. and *M. palustris* Aubl. of the Guianas.

